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Regional disparity in extinction risk: Comparison of disjunct plant genera between eastern Asia and eastern North America

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Abstract

Climate and land cover changes are increasing threats to biodiversity globally. However, potentially varying biotic sensitivity is a major source of uncertainty for translating environmental changes to extinction risks. To reduce this uncertainty, we assessed how extinction risks will be affected by future human-driven environmental changes, focusing on 554 species from 52 disjunct plant genera between eastern Asia (EAS) and eastern North America (ENA) to control for differences in environmental sensitivity at the genus level. Species distribution models were used to estimate and compare the vulnerability of species in disjunct genera between the two regions under two climate and land cover change scenarios (RCP2.6 and RCP8.5) in the 2070s, allowing to assess the effects of differences in climate and land cover pressures. Compared with ENA, stronger pressures from climate and land cover changes along with smaller range sizes in EAS translate into a larger number and proportion of species in disjunct genera becoming threatened by the 2070s. These regional differences are more pronounced under a best-case climate scenario (RCP2.6), illustrating that strong climate change (RCP8.5) may override any regional buffer capacities. The main variables determining extinction risks differed between the two continental regions, with annual temperature range and cropland expansion being important in EAS, and annual precipitation being important in ENA. These results suggest that disparities in regional exposure to anthropogenic environmental changes may cause congeneric species with relatively similar sensitivity to have different future risks of extinction. Moreover, the findings highlight the context-specific nature of anthropogenic effects on biodiversity and the importance of making region-specific policies for conservation and restoration in response to the intensifying global changes.

1 | INTRODUCTION

According to the latest biodiversity assessments of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the International Union for Conservation of Nature (IUCN), species extinction risk is accelerating globally (IPBES, 2019; IUCN, 2019). Increasing rates of human-driven habitat loss and climate change are recognized as two of the primary drivers of the observed and forecasted acceleration in species extinction (Newbold, 2018; Peters et al., 2019; Trisos et al., 2020). Although more and more studies have been focusing on the effects of climate and land cover changes on species loss, how future human-driven changes to the environment will translate into extinction risks (Hannah et al., 2020; Urban, 2015) remains unknown.

Extinction risks are the result of multiple interacting factors (Kling et al., 2020; Parmesan, 2006), including disparities in species' exposure to anthropogenic environmental changes and differences in species' sensitivity to climate change across different biotas (Cardinale et al., 2018; Dawson et al., 2011; Sax & Gaines, 2003). One way to separate the effects of these factors is to compare areas experiencing different magnitudes of anthropogenic pressures while controlling for differences in biotic sensitivity to these changes. In this circumstance, differences in regional extinction risks would purely reflect disparities in exposure to anthropogenic pressures.

Here, we use this approach to control for the differences in sensitivity and use the gradient in future exposure to environmental change across continents to assess how these may drive disparities in extinction risks. Specifically, we control for differences in biotic sensitivity by focusing on congeneric species from disjunct plant genera in eastern Asia (EAS) and eastern North America (ENA) due to the niche in conservatism at the genus level and the conservation of niche above the species level that are critically important for conserving biodiversity (Hadly et al., 2009). Hereby, this system serves as a natural experiment for assessing the link between environmental changes and extinction risks. The EAS–ENA disjunct genera originated from the same Arcto-Tertiary flora, broadly distributed across the Northern Hemisphere during the Paleogene and Neogene (Tiffney, 1985; Wolfe, 1975), but now only occur in EAS and ENA. This group of plants contributes to the high floristic similarity between EAS and ENA, stimulating important correspondence between Charles Darwin and Asa Gray due to the floras of EAS and ENA being more similar to each other than either was to western North America based on the floristic data available at that time (Boufford & Spongberg, 1983). Although the EAS–ENA disjunct genera are currently distributed in different latitudes within each continental region, climate associations of species within each EAS–ENA disjunct genus are well matched between the two continental regions (Qian et al., 2017; Qian & Ricklefs, 2004; Ricklefs & Latham, 1992), even though the disjunct populations have been separated between the two continents for millions of years (Wen, 1999). The EAS–ENA disjunct genera have served as a "model" system in addressing ecological and biogeographic questions (e.g., Qian & Ricklefs, 2000, 2004; Ricklefs & Latham, 1992), particularly for questions that require accounting for ecological differences between the compared groups (Qian & Ricklefs, 2000; Qian et al., 2007). Therefore, the well-documented niche conservatism in EAS–ENA disjunct genera at the genus level (e.g., Qian & Ricklefs, 2004; Ricklefs & Latham, 1992) can be translated into a fixed biotic sensitivity to environmental changes (notably in climate), allowing for a robust test of the effect of exposure on vulnerability.

To assess species extinction risks during the Anthropocene, it is important to consider the combined effects of climate and land cover changes (Titeux et al., 2016). Their combined effects are expected to cause elevated risks in species extinction and potentially major changes in the regional patterns of species richness (Newbold et al., 2019; Urban, 2015; Zhang et al., 2017). Thus, we considered climate and land cover changes simultaneously in the present study. Importantly, climate and land cover changes show different trends in EAS and ENA (Loarie et al., 2009; Newbold et al., 2015) due to disparate human population growth trends and differences in economic development (Guo, 1999; Seto et al., 2011). Notably, under a business-as-usual scenario, EAS is expected to experience larger precipitation and lower temperature changes across this century than ENA (Loarie et al., 2009). Moreover, faster rates of urban expansion in the next decades are expected in EAS, compared to ENA (Seto et al., 2012). The difference in the expected changes in climate and land cover between the two regions implies regional differences in species' exposure to these stressors.

In this study, 554 species from the 52 plant genera disjunctly distributed between EAS and ENA are used to determine differences in species extinction risks. We compare the range responses of these species under two greenhouse gas emission scenarios for the 2070s. For this, we model and compare current and future distributions of the 554 species, hereby determining regional differences in extinction risks of species in the 52 disjunct genera, while controlling for differences in sensitivity to climate and habitat changes. Based on the observed differences in climatic and land cover changes between EAS and ENA, we expect that extinction risk will be higher in EAS than in ENA due to expected stronger future shifts in climate (Loarie et al., 2009) and ongoing rapid land degradation (Seto et al., 2011, 2012) in EAS. Support for these predictions would highlight the need to make region-specific policies for biodiversity conservation and restoration under future global change.

2 | MATERIALS AND METHODS

2.1 | Study areas

We referenced the previous literature (Qian & Ricklefs, 2000) to define the geographic boundaries of EAS and ENA. EAS (18–55°N, 92–145°E) includes the majority of China (except for the provinces of Xinjiang, Gansu, Qinghai, Ningxia, and some counties of Xizang and Inner Mongolia), South Korea, North Korea, Japan, and the southernmost part of the Russian Far East (including Bureja, Daurian, Lower Zea, South Sakhalin, Ussuri). ENA (24–53°N, 57–100°W) includes the eastern parts of six states of the United States, including North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas, and all the states east of them as well as New Brunswick and Nova Scotia provinces and southern parts of Quebec and Ontario provinces in Canada.

2.2 | Species distribution data

We focused on the species of disjunct plant genera in EAS and ENA (Qian & Ricklefs, 2000). We only included occurrence records within the native range of each species. Data for species in China were compiled from several sources with occurrences primarily at the county level or smaller geographic areas (such as nature reserves), which included NSII (China's National Specimen Information Infrastructure, http://www.nsii.org.cn), GBIF (Global Biodiversity Information Facility, www.gbif.org), and a dataset reported in Lu et al. (2018). Data for species distributions in Korea were compiled from Lee (1980) and Lee (1996), Flora of Korea Editorial Committee (2015–2016), and distributional records with GBIF. Data for species distributions in Japan were compiled from Kubota et al. (2014), Nakamura et al. (2009), local and prefecture floras (http://jousyuu2.sakura.ne.jp/sankoubunken.html), and distributional records with GBIF. Data for species distributions in the Russian Far East were compiled from Charkevicz (1985–1996). Data for species distributions in the United States and Canada were compiled from county-level distributions with the databases of the Biota of North America Program (http://bonap.org) and the U.S. Department of Agriculture's Plants (https://plants.sc.egov.usda.gov/java/), and a large body of the botanical literature cited in appendix A in Qian et al. (2007). All species names were standardized following World Flora Online (www.worldfloraonline.org).

Under the Behrmann cylindrical equal-area projection, we divided the two regions into 50 km ×50 km grid cells (approximately equal to the size for most counties in the two continental regions). Only species with ≥5 occurrence records within a region were retained in the analyses to ensure the predictive ability of species distribution models (SDMs; Pearson et al., 2007). As a result, this study included 554 species (accounting for 97% of total species number) from 52 disjunct plant genera (Dataset S1), with 451 species in EAS and 104 species in ENA. There are no species in these genera that are currently shared by the two continental regions

except for *Phryma leptostachya*, for which EAS and ENA each possess a different subspecies. Among them, 78% (350 species) in EAS and 61% (63 species) in ENA are woody plants, and 22% (101 species) in EAS and 39% (41 species) in ENA are herbaceous plants. To compare climatic niches of the disjunct genera between the two continental regions at the genus level, we mapped the occupied area of the currently climatic space (mean annual temperature [MAT] vs. total annual precipitation [PREC]) between EAS and ENA (Figure S1). Figure S1 shows that many disjunct genera have relatively similar climate associations between the two continental regions, suggesting high similarity in climatic requirements and hence sensitivity at the genus level.

2.3 | Environmental variables

Current (1950–2000) and future (2061–2080) climate variables in EAS and ENA at 10 arc-minutes were obtained from the WorldClim database (Hijmans et al., 2005). For future climate, the BCC-CSM1-1, CCSM4, and GFDL-CM3 coupled global climate models, which are widely used for predicting species extinction risk in East Asia and North America (Stralberg et al., 2015; Tang et al., 2018; Zhang et al., 2017), were adopted under two levels of greenhouse gas emission scenarios by the 2070s: RCP2.6 as low level (global mean temperature will stabilize at ~1.6°C higher than the preindustrial period, which is close to the 1.5°C climate target) and RCP8.5 as high level (~4.8°C higher in temperature than the preindustrial period).

Current and future land cover data were extracted from Land-Use Harmonization (LUH2, http://luh.umd.edu; Hurtt et al., 2011). It consists of estimates of the land cover proportion at 0.25° resolution for the years 850–2100. We reclassified 12 LUH categories into five major types, including forested, non-forested, crop, urban, and grazing lands. Elevational range was used in this study as a proxy of habitat heterogeneity (Rahbek & Graves, 2001). Elevation data were obtained from the EarthEnv-DEM90 digital elevation model at 90 m resolution (http://www.earthenv.org/DEM). All these environmental variables were disaggregated to a 50-km spatial resolution. To reduce multicollinearity, the variables with the absolute value of Pearson correlation coefficient <0.7 were retained (Dormann et al., 2013). Finally, five climate variables (MAT, PREC, temperature annual range [TEMP_range], mean temperature of the wettest quarter [TEMP_wet], and precipitation seasonality [PREC_season]), five land cover variables, and elevational range were used in this study.

2.4 | Species distribution models

Species distribution models have been widely used to project the potentially suitable habitats and extinction risk of species (Elith & Leathwick, 2009; Rosenzweig et al., 2008). In this study, an ensemble of four SDM algorithms (maximum entropy, generalized linear models, generalized boosting model, and random forest; Moat et al., 2019; Razgour et al., 2019; Zhang et al., 2017) was used to project suitable

habitats under current and future RCP2.6 and RCP8.5 scenarios by the 2070 s. To evaluate and calibrate each model, we randomly divided our data into two parts: 80% of the initial data were used as training data to build models and the remaining 20% of the data were used to validate the models (Franklin & Miller, 2010) and then used true skill statistic (TSS) to evaluate the predictive accuracy of models (Allouche et al., 2006). To effectively balance between omission and commission errors in model prediction, this procedure was repeated five times for species with >1000 occurrence records, and 10 times for all other species (Barbet-Massin et al., 2012). We generated five sets of pseudo-absences by randomly selecting absence with the same number as presence records from the whole study area (Barbet-Massin et al., 2012). All calibrated models with TSS larger than 0.5 were retained (Thuiller et al., 2009; Figure S2). These retained models were then projected under the current conditions and under the two RCP scenarios for the 2070 s at a 50-km spatial resolution, using ensemble forecasting classified into binary presence–absence predictions of suitable habitat using the threshold that maximize TSS (Gallien et al., 2010). All functions for SDMs and ensemble forecasts were carried out using the R package "BIOMOD2" (Thuiller et al., 2009).

Considering that the SDMs commonly overpredict distributions, we used a buffered minimum convex polygon (MCP) to clip the SDM range predictions following the approach of Kremen et al. (2008). For current conditions, 200 km was considered as an "optimal" MCP buffer distance (VanDerWal et al., 2009). For future conditions, we extended the distance based on a maximum dispersal rate of 20 km per decade, starting at the buffer edge (Chen et al., 2011). This analysis was performed using the "gConvexHull" and "gBuffer" functions in the R package "rgeos" (https://r-forge.r-project.org/projects/rgeos).

2.5 | Statistical analysis

To investigate the shifts in species richness between the current and future periods, we mapped the changes in species richness based on the binary models of potentially suitable habitats. To detect the expected direction and distance of range shifts of each species, we calculated the location of the geographic center (centroid) of each species' range for current and future periods, and the directions and distances were measured based on the changes between current and future centroid. This analysis was conducted using the function "gCentroid" in the R package "rgeos."

The percentage loss of current suitable habitat (LSH) and relative change in total area of suitable habitat (CSH) was used as the proxy of species' vulnerability to future climate and land cover changes (Thuiller et al., 2011). LSH and CSH were calculated as follows: $LSH = 100 - (overlap(AREA_{Future}, AREA_{Current})/AREA_{Current} \times 100)$, and $CSH = (AREA_{Future} - AREA_{Current})/AREA_{Current} \times 100$, where $AREA_{Future}$ and $AREA_{Current}$ are the area of future and currently suitable habitats, respectively. To estimate and compare species extinction risks between the two regions, we calculated the number of species and the proportion of total species under greater than 30%, 50%, and 80% of LSH and CSH. Species extinction risk in

each region was defined as the percentage of species that have lost over 30% of their suitable habitat (IUCN, 2019). We also summarized changes in species range (CSH) due to climate and land cover changes across a genus-level phylogeny for the EAS–ENA disjunct genera, which was extracted from the megaphylogeny reported by Smith and Brown (2018).

To disentangle potential drivers of extinction risk in the two regions, beta regression in R package "betareg" (Cribari-Neto & Zeileis, 2010) was used to explore the bivariate relationships between LSH and each explanatory variable at the species level. Beta regression is commonly used to model proportional data restricted between 0 and 1 that are typically non-normal and heteroscedastic (Cribari-Neto & Zeileis, 2010). The explanatory variables were computed as changes in predictors between the current and future periods. For each species, the change in each variable used for beta regression is the average in difference of all grids with losing suitable habitats between current and future predictions. To eliminate the unit dimensions of predicted variables for comparing their relative importance, all variables were standardized to have a mean of 0 and standard deviation of 1.

To test for differences in loss of range sizes among congeneric species between the two regions, we conducted a pairwise phylogenetic generalized least squares analyses of $\log_{10}$-transformed current and loss of range size of the 52 disjunct genera shared by the two regions. This method accounts for the nonindependence of species in the same genera. This analysis was implemented with the R package "ape" (http://ape-package.ird.fr). A chi-squared test was used to evaluate the correlation of range size loss between the two regions. All the data were prepared and analyzed in R v3.6.3 (R Core Team, 2019).

3 | RESULTS

3.1 | Geographical shifts in species richness

Under the RCP8.5 scenario, the net losses in species richness in EAS and ENA were 123 (27%) and 21 (20%) species per 50 km ×50 km grid cell, respectively (Figure 1). Under the two evaluated scenarios for the 2070s, the largest species loss was projected to be at low latitudes (below 30°N) in EAS and mid-low latitudes in ENA (below 40°N; Figure 1) and some grid cells were projected to lose all species (Figure S3). Southern and southwestern parts of EAS and the Mississippi coastal plain in ENA were also predicted to have large declines in species richness. Notably, under RCP8.5 in EAS, 19 and 13 species were predicted to lose all their suitable habitat and become regionally extinct under the assumption of no migration and universal migration, respectively.

3.2 | Disparate species extinction risks of disjunct genera between EAS and ENA

Under the RCP8.5 scenario, 49% and 39% species in the disjunct genera in EAS and ENA would be at risk of extinction (LSH >30%)
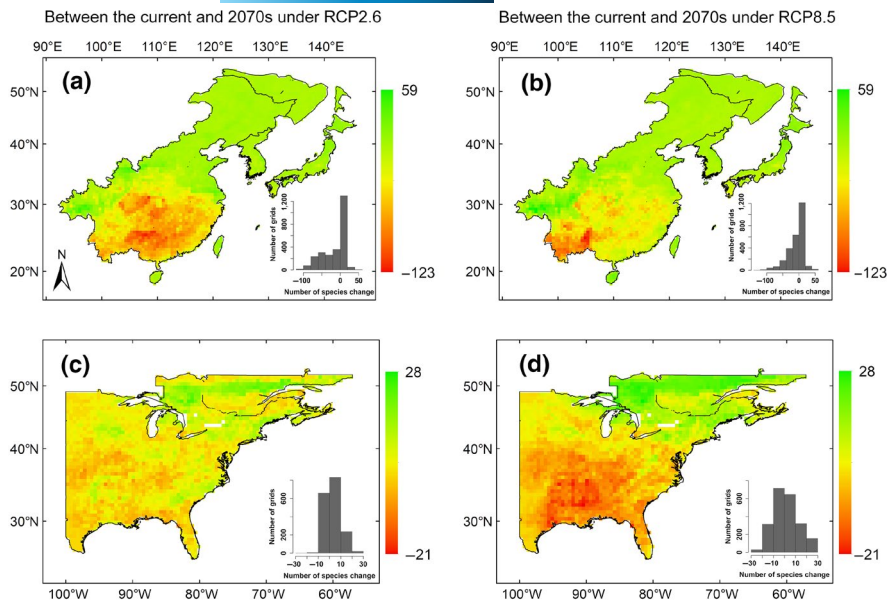
FIGURE 1 Forecasted changes in species richness of the disjunct plant genera between the current (the 2000s) and the 2070s under two greenhouse gas emission scenarios for eastern Asia (EAS; a, b) and eastern North America (ENA; c, d). The species distribution model results under universal migration are shown here, hence representing potential ranges. The histograms (bottom-right insets) show the frequency of species richness change between the current and the 2070s [Colour figure can be viewed at wileyonlinelibrary.com]
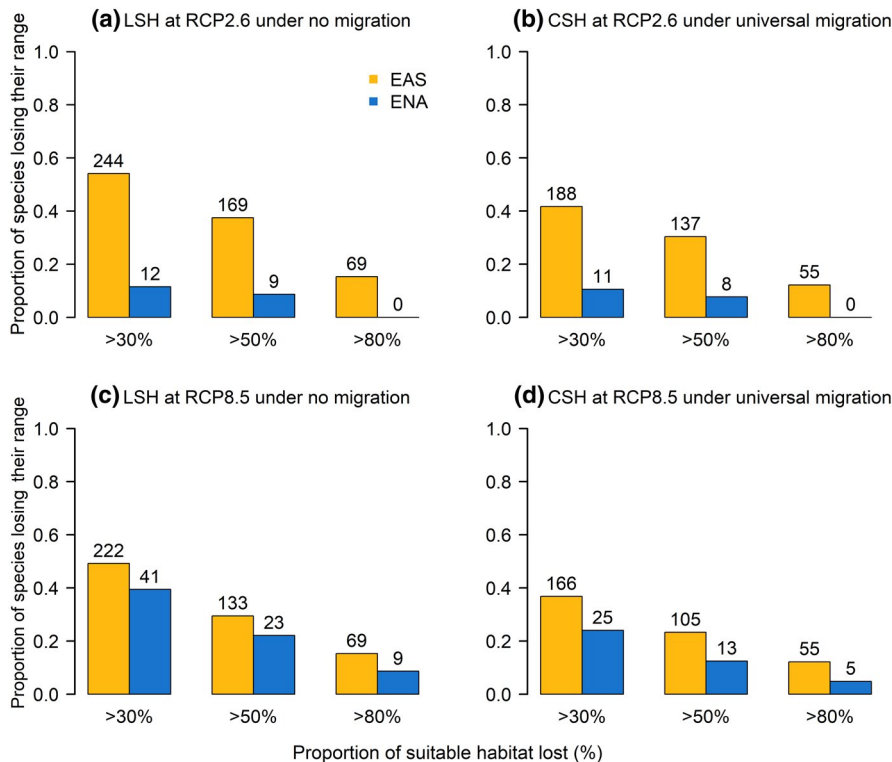

FIGURE 2 The proportion of modeled suitable habitat loss of species by the 2070s under two emission scenarios. The left column is the relative loss of current suitable habitat (LSH) assuming no migration, and the right one is the relative change of suitable habitat (CSH) assuming universal migration. The number above the bar is the number of species losing their range. EAS, eastern Asia; ENA, eastern North America [Colour figure can be viewed at wileyonlinelibrary.com]

by the 2070s, respectively (Figure 2). Differences in the proportion of species at extinction risk between EAS and ENA are more pronounced under a best-case climate scenario (RCP2.6) for both LSH (54% in EAS vs. 12% in ENA) and CSH (42% in EAS vs. 11% in ENA; Figure 2a,c). The analysis of CSH across a genus-level phylogeny (Figure 3) confirmed that changes in the suitable habitat will differ between the two regions for most of the disjunct genera, with those in EAS experiencing larger reductions than their counterparts in ENA (most pairs under the 1:1 line in Figure 4d,e).

3.3 | Drivers of regional disparity in species extinction risks

In EAS, the changes in annual temperature range, cropland, and non-forest expansion showed positive relationships with LSH (Table 1). In contrast, in ENA, LSH was significantly and positively associated with annual precipitation and cropland. Moreover, human pressures have greater impacts on LSH in EAS due to the higher human anthropogenic pressure in this region (Table 1; Figures S4 and S5). For example, under a high-emission scenario (RCP8.5), EAS will experience

greater intensification of land uses, and a much larger expansion in non-forest and cropland when compared with ENA. For urban land, although the rate of urban expansion is lower in EAS than in ENA, EAS will mostly experience greater expansion extent than ENA.

For most congeneric species, the range size of a species in the same disjunct genus is larger in ENA than in EAS under both current and future conditions (Figure 4a–c). There were significant correlations between LSH of congeneric species in the two regions, yet the genera in EAS are forecasted to experience a larger loss in species range size. In addition, LSH was reduced with increasing range size in both regions, but with a sharper reduction in ENA (Figure 5). A similar result of all study species in two regions was documented (Figure S6).
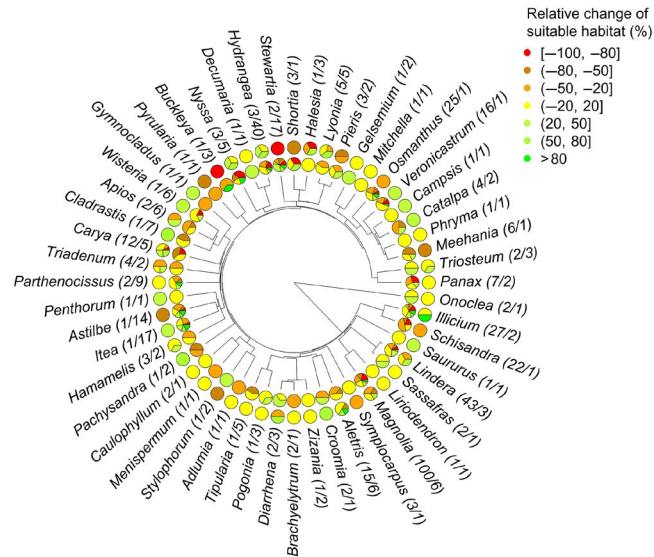
4 | DISCUSSION

The highly elevated rates of species loss due to human pressures continues to raise concern (e.g., IPBES, 2019), yet the link between environmental changes and species extinction risk is still poorly understood. One complicating factor is the potential for regional differences in biotic sensitivity to environmental changes (Cardinale et al., 2018; Dawson et al., 2011). In this study, we took a natural experiment approach to assess whether regional differences in intensity in environmental changes drive disparity in species extinction risks, controlling for differences in biotic sensitivity at the genus level. Our analyses showed marked differences in extinction risks as well as clear differences in potential drivers of extinction risks between the two study regions, consistent with different magnitudes of environmental changes. Compared with ENA, stronger pressures from climate and land cover changes along with smaller range sizes in EAS translated into a larger number and proportion of species in this region projected to become threatened by the 2070s.

The impacts of climate and land cover changes on biodiversity have been predicted to vary markedly across different regions (Newbold et al., 2019). Our results provide evidence for regional differences in extinction risks of species, in line with previous studies (Collen et al., 2006; Thomas et al., 2004; Thuiller et al., 2005; Urban, 2015), but here these differences can be clearly attributed to dissimilarities in exposure to anthropogenic pressures by controlling for
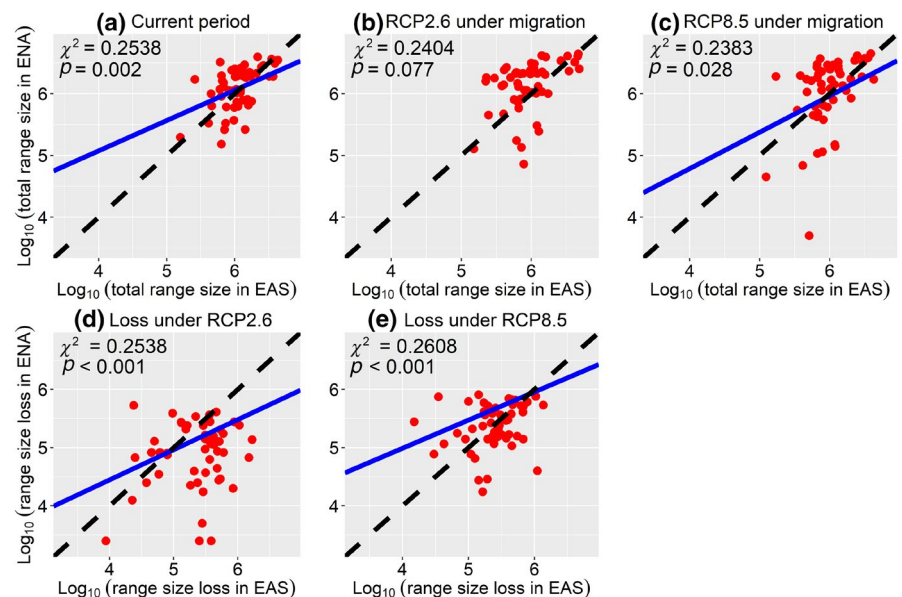

FIGURE 3 Projected species changes in all EAS–ENA disjunct plant genera between the current and the 2070s (RCP8.5). Genus names are labeled on the phylogeny. Colors in pie charts show the percent of species relative to species richness within each of seven different habitat change levels. The inside pie charts represent EAS species, and the outside charts represent ENA species. Two numbers in parentheses after a genus name are the numbers of species in EAS (the internal number) and ENA (the external number). "(" and "]" mean that the boundary value is not included and included in the division interval, respectively. EAS, eastern Asia; ENA, eastern North America [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Scatter plots showing the relationships of current range size (a), and future range size (b, c) as well as range size loss under two emission scenarios (d, e) between the two regions. EAS, eastern Asia; ENA, eastern North America [Colour figure can be viewed at wileyonlinelibrary.com]

	EAS			ENA		
	Coef.	Odds ratio (CI)	Pseudo r^2	Coef.	Odds ratio (CI)	Pseudo r^2
TEMP_range	1.046***	2.85 (2.38–3.41)	0.175	0.078	1.08 (0.65–1.81)	0.000
PREC	−0.114	0.89 (0.77–1.03)	0.001	0.892***	2.44 (1.95–3.05)	0.262
Non-forest cover	1.356***	3.88 (2.84–5.32)	0.019	−0.053	0.95 (0.82–1.09)	0.014
Urban cover	−0.316***	0.73 (0.62–0.86)	0.046	0.379	1.46 (0.73–2.91)	0.011
Cropland cover	1.723***	5.60 (4.30–7.29)	0.207	0.671*	1.96 (1.04–3.69)	0.040

TABLE 1 Bivariate relationships between the percentage of current suitable habitat loss (LSH) of the species in the EAS–ENA disjunct plant genera and changes in the explanatory variables based on beta regression models under RCP8.5 emission scenario in eastern Asia (EAS) and eastern North America (ENA)
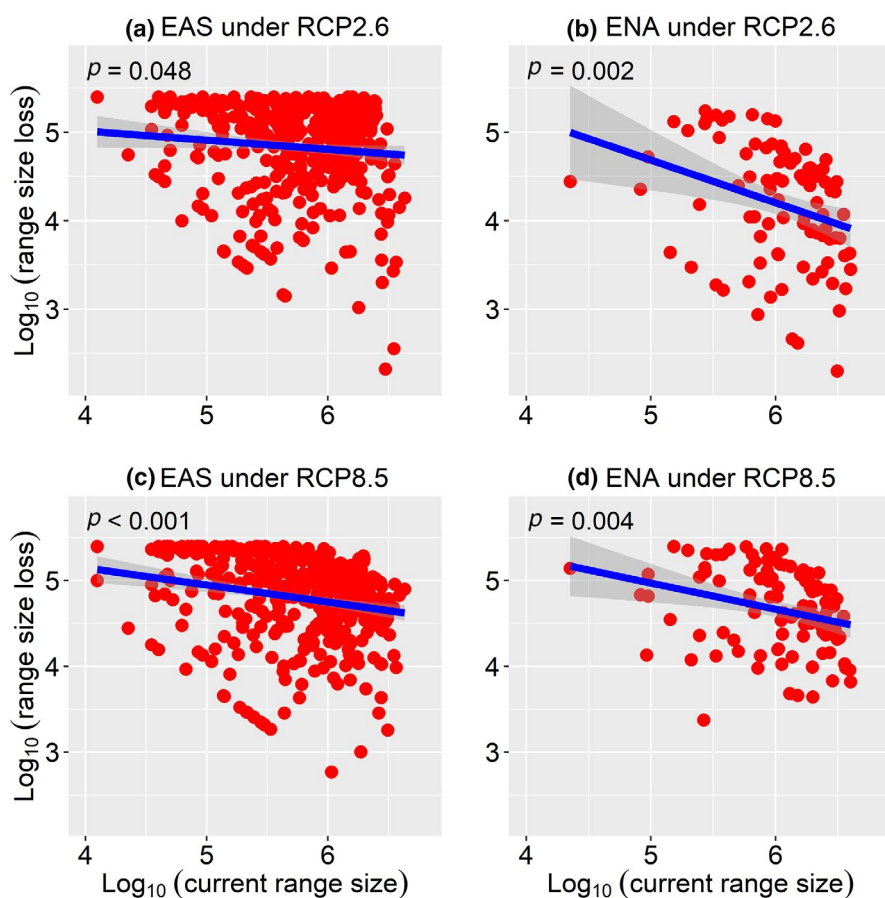
Note: Standardized regression coefficients (Coef.) and pseudo r^2 are given.

Abbreviations: CI, confidence interval; PREC, annual precipitation; PREC_season, precipitation seasonality; TEMP_range, temperature annual range.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

FIGURE 5 Scatter plots showing the relationships between range loss and current range size under RCP2.6 (a, b) and RCP8.5 (c, d) in eastern Asia (EAS) and eastern North America (ENA) [Colour figure can be viewed at wileyonlinelibrary.com]

biotic differences via focusing on EAS–ENA disjunct plant genera. The discrepancy of forecasted species loss in the disjunct genera between EAS and ENA is most pronounced under the low-emission scenario RCP2.6. This likely reflects that the high-emission scenario (RCP8.5 in our study) constitutes a generalized ecological disruption due to the exposure of most species to climate conditions exceeding their realized niche limits. In this case, environmental pressures are so severe that they overwhelm regional differences in buffer capacity (Trisos et al., 2020).

There were clear differences in the effects of climate change as drivers of extinction risks between EAS and ENA. Although the main areas of species loss in southern parts of both regions are expected due to the fact that EAS–ENA disjunct taxa tend to occupy temperate regions (Qian & Ricklefs, 2000), the climatic drivers of species

loss are different. In EAS, the main areas of species loss are those located in areas with large increases in annual temperature range (Figures S4 and S5) and are not affected by changes in precipitation. In contrast, in ENA, annual precipitation drives the relative loss of currently suitable habitats (Table 1; Figures S4 and S5). Our results coincide with the prediction by Pelletier et al. (2018) that the importance of annual temperature range on species loss is larger in Asia than that in North America.

Changes in land cover in both regions contribute critically to the loss of suitable habitats. The expansions for cropland and non-forest land were confirmed to increase the loss of suitable habitats in EAS, with the role of cropland much the strongest (Table 1). One reason for this is the rapidly growing human population (Feng et al., 2017) and future continuous expansion of cropland due to intensive agricultural technologies in EAS. These changes will result in further biodiversity decline due to substantial loss of natural habitats and increases in habitat fragmentation (Seto et al., 2012). In ENA, increasing cropland also drives species extinction risks, but here the contribution of cropland is far less than the contribution of precipitation. In EAS, urban expansion has a moderate effect on the extinction risk of species in the disjunct genera. This likely reflects that the regions with high risks (e.g., mountainous areas of southwestern China) are forecasted to be largely unaffected by urbanization directly (Figures S4 and S5), consistent with the global forecasts of patterns of urban expansion by Seto et al. (2012). In addition, there was a slightly higher risk of species extinction with LSH >30% or >50% in EAS under RCP2.6 than under RCP8.5. One possible reason is that the extent and intensity of land cover change (e.g., cropland expansion) in some regions of EAS under RCP2.6 are projected to be stronger compared with that under RCP8.5 (Figures S4 and S5), which leads to higher extinction risks of some species. Overall, although land cover variables play relatively minor roles in determining current species distributions in both regions, future expansions of land cover are expected to play an increasingly important role in raising species extinction risks (Newbold, 2018; Newbold et al., 2015).

Species range size influences the resilience to human pressures and climate fluctuations and has been widely used to assess species extinction risk (Davies et al., 2009; IUCN, 2019). Building on the assumption of relatively similar sensitivity to environmental changes of the EAS–ENA disjunct genera due to niche conservatism (Qian & Ricklefs, 2004), we expect that the loss of suitable habitat would be different when facing different degrees of anthropogenic threats. As expected, species extinction risk is reduced with increasing range size in both regions. Compared with ENA, for most congeneric pairs, EAS has more species with small range size. Small-ranged species are more vulnerable to extinction under climatically unstable areas, as they often have small population sizes and are less likely to occupy remaining suitable habitats during climate oscillations (Jansson, 2003). This result highlights the importance of small-ranged species in the assessment of species extinction risk.

Consistent with previous studies (e.g., Hickling et al., 2005, 2006; Zhang et al., 2017), our results show that the largest species loss of

the disjunct plant genera was projected to be at low latitudes. Most regions at low latitudes are expected to be warmer in the 2070s (Figures S4 and S5), resulting in the loss of suitable habitats for these temperate-zone species. It is particularly important to note that an excess of species loss is expected in the mountain regions of southern and southwestern China. This is inconsistent with the findings by Tang et al. (2018) that reported that these regions continue to be the refuge of plant species under future climate changes. The discrepancy between the two studies may reflect differences in the plant groups covered, but potentially also the coarser spatial grain of our analyses. On the one hand, our work focuses on species in the EAS–ENA disjunct genera, while Tang et al. (2018) focused on relict plant species even though 8% of these species are the same as ours. For many species of the disjunct genera in EAS, the southern and southwestern mountains are low-latitude range boundaries that may be sensitive to climate warming and habitat loss, and the narrow habitat tolerances of the mountain flora, in conjunction with marginal habitats for many disjunct genera species, are likely to promote high rates of species decline (Franco et al., 2006; Thuiller et al., 2005). On the other hand, the relatively coarse grid scale of our study may not reliably account for habitat heterogeneity of mountains and hide potential refuges for species (Guisan & Theurillat, 2000; Thuiller et al., 2005). Although mountainous areas may have higher scope for providing microrefugia than those identified in the present study, their small size would still represent an increased vulnerability to pressures such as from further broad-scale climate change.

In summary, our results show that despite the overall high similarity in climatic sensitivity between the species of the EAS–ENA disjunct plant genera, the floras of these two regions would expect to have different fates under the future changes in climate and land cover, with higher extinction risk in EAS. An increasing number of species are projected to become vulnerable to anthropogenic changes in the coming decades (IPBES, 2019; Newbold, 2018; Peters et al., 2019). Here, we show that this vulnerability is not homogeneous across regions, with stronger pressures along with smaller range sizes behind the greater extinction risks in EAS. These results highlight that different environmental settings and pressures may cause species with similar sensitivity to have different future risks of extinction in different regions. From a conservation perspective, this calls for region-specific policies for conservation and restoration, with stronger efforts being needed in some regions. Meanwhile, our results also indicate that strong climate change may overwhelm any such regional differences in buffer capacity, and highlight the importance of minimizing future climate change under the ongoing acceleration of biodiversity crisis.

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SUPPORTING INFORMATION

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