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Extinction risk of North American seed plants elevated by climate and land-use change

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Summary

1. Climate and land-use change are expected to substantially alter future plant species distributions leading to higher extinction rates. However, little is known about how plant species ranges, richness and phylogenetic diversity of continents will be affected by these dynamics.

2. We address this gap here by examining the patterns of species' distributions and phylogenetic relationships for 7465 seed plant taxa in North America. An ensemble of species distribution models was used to estimate the potential suitable habitat of species under different sets of climate, land-use and dispersal constraint scenarios. We then evaluated the vulnerability and extinction risk of individual species to changes in climate and land use, and examined whether rare, endangered and evolutionarily distinct species were disproportionally threatened by climate and land-use change.

3. We show that ~2000 species may lose >80% of their suitable habitats under the A1b emission scenario for the 2080s, while ~100 species may experience >80% range expansions (a 20 : 1 ratio of loss to gain). When considering >50% range retraction and expansion, the ratio of loss to gain was 13 : 1. A greater loss of species diversity is expected at low latitudes, while larger gains are expected at high latitudes. Evolutionarily distinct species are predicted to have significantly higher extinction risks than extant species. This suggests a disproportionate future loss of phylogenetic diversity for the North American flora.

4. *Synthesis and applications*. Our study provides continental-scale evidence of plant species extinction risk caused by future climate and land-use change, and highlights the importance of integrating phylogenetic measures into conservation risk assessments. This work provides insight into the status, trends and threats for a large share of North America's plant species by identifying risks and prioritizing conservation in a rapidly changing world.

Key-words: climate refugia, endemism, ensemble forecast, evolutionary diversity, extinction, phylogenetic diversity, range shift, species distribution modelling

Introduction

To inform the efforts of the recently launched Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (http://www.ipbes.net) (Díaz *et al*. 2015), a greater understanding and the ability to forecast the effects of climate and land-use change on species ranges and diversity are needed (Pimm *et al*. 2014). The interplay between climate change and modifications in land use is expected to cause major changes in the patterns of species richness and species turnover, leading to greater risks in species extinction (IPCC 2014; Pimm *et al*. 2014; Urban 2015). To help with conservation planning efforts, a greater understanding of future biodiversity dynamics is needed at regional scales and for different taxonomic groups (e.g. Thomas *et al*. 2004; Thuiller *et al*. 2005, 2011;

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Sommer *et al.* 2010; Lenoir & Svenning 2015). However, most past work has focused on a single driver like climate change with much less attention given to the joint effects of climate and land-use change at larger spatial scales (e.g. continental or global scales) (Jetz, Wilcove & Dobson 2007; Thuiller *et al.* 2014; Lenoir & Svenning 2015). Plants form the foundation of ecosystems as they are responsible for the primary productivity that other terrestrial organisms rely on. Little, however, is known about how this group will be impacted at continental scales by joint future changes in climate and land use.

Species respond to changes in climate and land use in different ways. Some species may expand their distribution (ranges), while others experience their range loss or even go extinct (Parmesan & Yohe 2003; Kelly & Goulden 2008; Pimm *et al.* 2014). One consequence is the loss of phylogenetic diversity (Purvis *et al.* 2000; Thomas *et al.* 2001; Vamosi & Wilson 2008; Lavergne *et al.* 2010, 2013). Because closely related species are expected to have similar ecological niches (i.e. phylogenetic niche conservatism) (Araujo & New 2007; Wiens *et al.* 2010), impacts of environmental change may have a disproportionate effect on some closely related species or clades (Thuiller *et al.* 2011; Pio *et al.* 2014; Zhang, Huang & He 2015; Veron *et al.* in press). Phylogenetic niche conservatism may therefore result in greater risk for certain parts of the tree of life (Eiserhardt *et al.* 2015). However, existing assessments between phylogenetic diversity and climate change do not generally lead to consistent results, with some showing no phylogenetically biased extinction risk (Thuiller *et al.* 2011; Pio *et al.* 2014) and others strong phylogenetic signals (Eiserhardt *et al.* 2015). This may be due to the difference in spatial scale and phylogenetic breadth in different analyses. This has reinforced the debate of whether phylogenetic diversity should be considered in biodiversity conservation (Winter, Devictor & Schweiger 2013). We suggest that continental-scale analyses are needed to compare the response of phylogenetic diversity across different regions with different biogeographic histories to future climate and land-use change.

Here, we report on a comprehensive evaluation of the combined effects of climate and land-use change on 7465 plant taxa in North America, a continent with considerable ongoing and future land-use and climate change (IPCC 2014; Melillo, Richmond & Yohe 2014; Warren & Lemmen 2014). An ensemble of species distribution models (SDMs) was used to estimate the potential suitable habitat of individual species under different climate, land-use and dispersal constraint scenarios. We then used ensemble projections to evaluate the vulnerability and extinction risk of individual species to changing climate and land uses, and examined whether rare species, endangered species or evolutionarily distinct species were disproportionally threatened by climate and land-use change. Finally, we used phylogeny-based approaches to test whether these extinction risks were random with respect to the tree of life for North America's plant flora. Our study provides continental-scale evidence of future climate and land-use change on plant species extinction while also highlighting the importance of the integration of phylogenetic-related measures into conservation efforts.

Materials and methods

PLANT SPECIES

We assembled woody plant species data from the United States Forest Inventory and Analysis (FIA, http://www.fia.fs.fed.us) and Canadian permanent sampling plots (PSPs) in six provinces (British Columbia, Alberta, Saskatchewan, Manitoba, Ontario and Quebec). In each FIA site, all trees with a diameter at breast height (DBH) ≥12·7 cm and all saplings (DBH 2·5–12·7 cm) and seedlings (DBH <2·5 cm) were measured and recorded, together with the geographic locations of each site (Smith 2002). Each FIA site was composed of four circular 0·017-ha subplots and four 0·001-ha microplots. PSP sites in Canada also used similar field protocols with FIA, although there are some differences such as plot size and minimum measured DBH (Zhang, Huang & He 2015). In total, 19 891 PSP plots were used. The average size of these plots was 0·14 ha, ranging from 0·04 to 0·81 ha.

Since FIA and PSPs included only 546 woody plant species distributed in the USA and Canada, we added both woody and non-woody plant occurrence records from the GBIF data infrastructure (Global Biodiversity Information Facility, www.gbif.org) for USA, Canada and Mexico. GBIF is a comprehensive data base that holds over 440 million records of species occurrences from over 610 publishers (Yesson *et al.* 2007; Samy *et al.* 2013). Over 1000 peer-reviewed publications have used GBIF data (http://www.mendeley.com/groups/1068301/gbif-public-library). We combined species to a common synonym and cleaned data for the potential spatial errors (e.g. coordinates outside of North America or within large lakes and reservoirs) to minimize the errors in SDMs (Appendix S1, Supporting information).

In total, 7465 seed plant taxa from 1876 genera and 216 families were used, including 248 subspecies and 276 varieties (by taxa, we mean distinct species, subspecies or varieties, and we use 'species' hereafter for simplicity). We included subspecies and varieties since some subspecies and varieties have been well studied in North America (e.g. white basswood *Tilia americana* var. *heterophylla* and plains cottonwood *Populus deltoides* subsp. *monilifera*). Of these 7465 species, 7351 species are angiosperms and 114 species are gymnosperms (Table S1). The number of occurrences for each species ranged from 50 to 108 199 occurrence records aggregated within grid cells of a 20 × 20 km resolution. In total, 6156 species had occurrence records north of Mexico, while 3881 species had occurrence records in Mexico. To consider the implications of a possible sampling bias, we analysed North America and separately North America north of Mexico. Results were similar, so we report the results for the larger area in the main text with the results for North America north of Mexico presented in Fig. S6.

CLIMATE DATA

Climate variables of North America at 20-km spatial resolution were extracted from 4-km resolution ClimateNA data set (http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/) (Stralberg *et al.* 2015), which comprises 20 biologically relevant

variables, including seasonal and annual means, extremes, growing and chilling degree days, snow fall, potential evapotranspiration, climatic moisture deficit, climatic moisture index and summer climatic moisture index (Hamann *et al.* 2013). Climate variables for the 2050s (2041–2070) and 2080s (2071–2100) were also derived from the same ClimateNA data set. High variability in general circulation model (GCM) projections is a major source of uncertainty in predictive species modelling (Thuiller *et al.* 2005; Sommer *et al.* 2010). Two GCMs, coupled global climate model (CGCM, version 3.1, t47, Victoria, Canada) and GFDL's CM global coupled climate model (GFDL-CM, version 2.1, Washington, DC, USA), were selected for the 2050s and 2080s. These two GCMs have been recommended for use in North America, according to the results of validation ranks of 24 GCMs (Stralberg *et al.* 2015). For each GCM, we included two emission scenarios (A1b and B1). A1b scenario is for a future world with maximum energy requirements, and the B1 scenario is for a convergent world with lower energy requirements (Nakicenovic 2000).

LAND-USE DATA

Current (the year 2000) and future global land use and land cover at a 0·5-degree resolution were derived from the GLOBIO3 model, including 30 different land-use types (Alkemade *et al.* 2009). These land-use types were disaggregated to 20-km spatial resolution using nearest neighbour algorithm. For the two selected emission scenarios (A1b and B1), we reclassified the 30 land-use types into 12 general types by grouping similar land uses (Bellard *et al.* 2013). These land-use variables consisted of the proportion of the grid cell covered by (i) tree cover, (ii) tree cover regularly flooded, (iii) mosaic habitat, (iv) tree cover burnt, (v) shrub cover, (vi) herbaceous cover, (vii) cultivated and managed areas, (viii) bare areas, (ix) water bodies, (x) snow and ice, (xi) impervious and other non-natural surfaces and associated areas and (xii) pasture. We calculated for each pixel the proportion of each land-use type in three time periods (current, 2050s and 2080s), and used each as an independent predictor in SDMs for its corresponding time period.

VARIABLE SELECTION

To reduce the multicollinearity among environmental predictor variables, Pearson's correlations and variance inflation factors (VIFs) were used for variable selection (Marquardt 1970). Variables with a Pearson correlation >0·70 were considered highly correlated (Dormann *et al.* 2013), and a VIF >5 was used as a signal that a model had collinearity issues (Rogerson 2001). A preliminary analysis showed weak correlations between climatic variables and land-use variables, so we assessed multicollinearity separately. Finally, we selected five climate variables and five land-use variables for modelling species distributions. Climate variables included maximum temperature of warmest month, mean summer precipitation, winter precipitation, climatic moisture deficit and precipitation as snow, while land-use variables included tree cover, shrub cover, herbaceous cover, cultivated and managed areas, water bodies and pasture cover.

SPECIES DISTRIBUTION MODELS (SDMS)

An ensemble of SDM forecasts were obtained for each species (Araujo & New 2007). The ensemble included projections from four modelling algorithms: generalized additive models (GAM), boosted regression trees (BRT), random forest (RF) and maximum entropy (Maxent). Models were calibrated for the baseline period using a 80% random sample of initial data and evaluated for predictive accuracy against the remaining 20% of data using true skill statistics (TSS) (Allouche, Tsoar & Kadmon 2006; Marmion *et al.* 2009). TSS was calculated using this function: $TSS = sensitivity + specificity - 1$, which considers the measures of both sensitivity and specificity so that both omission and commission errors are accounted for (Allouche, Tsoar & Kadmon 2006). This procedure was repeated five times for species with a total number of occurrences lower than 100 or 10 times for all other species. Here, we only included the models that reached a TSS larger than 0·5 (Fig. S1). Five sets of pseudo-absences were generated by selecting the same number of random absences with the number of presences across the whole study area (Allouche, Tsoar & Kadmon 2006; Barbet-Massin *et al.* 2012). This threshold of 0·5 was selected according to the recommendation in the manual of the BIOMOD2 package (Thuiller *et al.* 2009). All calibrated models were then projected under current and future conditions at a 20-km resolution, and the ensemble forecast classified into binary presence–absence predictions of suitable habitat using the threshold that maximizes TSS (Gallien *et al.* 2010). All models and ensemble forecasts were performed within the BIOMOD2 package (Thuiller *et al.* 2009) in R language (R Core Team 2014).

As 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). This method produces predictions that represent a suitable habitat within an area of known occurrence (based on a buffered MCP), excluding the suitable habitat greatly outside of observed range and the unsuitable habitat through the landscape. For current conditions, we used 200 km as the MCP buffer distance. Based on a study on Australian vertebrates by VanDerWal *et al.* (2009), a 200-km buffer has been recommended as an 'optimal' distance to produce models that both generalize well across a range of environmental conditions and do not overinflate predicted distributions at finer environmental gradients. 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 'convHull' function in R package 'dismo' (http://cran.r-project.org/web/packages/dismo/index.html) and 'gBuffer' function in R package 'rgeos' (https://r-forge.r-project.org/projects/rgeos).

To detect the direction and distance of changes in species ranges in future conditions, we calculated the location of the geographic centre of each species range extant for current and future periods, and the directions and distances were measured based on the changes between current and future centroid. This analysis was performed using 'gCentroid' function in R package 'rgeos'. All summaries of changes in area and distance of species distribution used trimmed SDM predictions with a Lambert conformal conic equal-area projection.

PHYLOGENY CONSTRUCTION

We adopted several previous studies (Thuiller *et al.* 2011; Roquet, Thuiller & Lavergne 2013; Zanne *et al.* 2014) to develop both genus- and species-level phylogenetic supertrees for North American plant species. First, we generated a genus-level megaphylogeny for 8179 genera based on the recently established species-level phylogeny supertree for 31 749 plant species by Zanne *et al.* (2014). This genus-level phylogeny included 1699 genera of

our North American plant species, but did not include 177 other genera. For these missing genera, we used an imputation method to add these genera into the supertree by using a family tree (Qian & Zhang 2014). We added the genera to the phylogeny as polytomies of the basal genus within its family. Finally, we pruned this genus-level phylogeny into a genus-level phylogeny for all 1876 genera in our study taxa. To build a species-level phylogeny, we used the updated version of the R function 'stickTips', which was developed by Roquet, Thuiller & Lavergne (2013). We randomly resolved terminal polytomies by applying a birth–death (Yule) bifurcation process within each genus and repeated this process 100 times with 100 estimated phylogenies generated for our study taxa (Roquet, Thuiller & Lavergne 2013).

MEASURES OF SPECIES' VULNERABILITY

We quantified species' vulnerability to future climate and land-use change using two metrics: (i) relative change in the total area of suitable habitat (CSH) and (ii) percentage loss of current suitable habitat (LSH) (Thuiller *et al.* 2011). CSH and LSH were calculated as follows: $CSH = (AREA_{Future} - AREA_{Current})/AREA_{Current} \times 100$, and $LSH = 100 - (\text{overlap } (AREA_{Future}, AREA_{Current})/AREA_{Current} \times 100)$, where $AREA_{Future}$ is the area of future suitable habitats and $AREA_{Current}$ is the area of current suitable habitats. These metrics were calculated for the two time periods, emission scenarios and climate and land-use models. We further classified the 7465 species into different groups of rarity to evaluate whether rare and common species responded differently to climate and land-use change. First, we classified the 7465 species into six categories of rarity based on the number of 20-km grids the species occurred in (N_{grid}). These six categories of rarity included: (i) very rare ($N_{grid} \leq 10$), (ii) rare ($10 < N_{grid} \leq 20$), (iii) few common ($20 < N_{grid} \leq 50$), (iv) moderately common ($50 < N_{grid} \leq 100$), (v) common ($100 < N_{grid} \leq 500$) and (vi) very common ($N_{grid} \geq 500$). Secondly, we used IUCN (International Union for Conservation of Nature) Red List of Threatened Species (IUCN 2014) and NatureServe global level rank (Natureserve 2014) to classify the conservation status of species, although conservation information for some species was unknown (354 species in the IUCN Red List and 5408 species in the NatureServe data base). The latter were excluded from this comparison, but still used in all other analyses.

To evaluate whether phylogenetically related species have similar responses to environmental change, we first used a phylogenetic signal test of species' vulnerability (CSH and LSH). We used the two widely used phylogenetic signal indices of Abouheif's *Cmean* (Abouheif 1999) and Blomberg's *K* (Blomberg, Garland & Ives 2003). For each of 100 phylogenies, each test was performed with 99 randomizations. Secondly, we analysed the relationship between species' vulnerability and evolutionarily distinctiveness (ED) which measured how isolated a species was on its phylogenetic tree (Redding & Mooers 2006). This index was calculated for each of 100 phylogenies. Average ED of each species was used to test whether the species with larger evolutionarily distinctness were more threatened than others compared with changes in range size.

EFFECTS OF CLIMATE AND LAND-USE CHANGE ON PHYLOGENETIC DIVERSITY

We used two approaches to test whether the losses of plant phylogenetic diversity are random on the tree of life for North American plants. First, following Thuiller *et al.*'s (2011) approach, we used CSH as surrogates for probability of extinction and weighted the edge length of each phylogenetic tree by the expected survival probabilities of each species under each time slice and scenario. The expected values of Faith's phylogenetic diversity (PD) (Faith 1992) were compared to the PDs generated by 99 replicates which randomized the CSH across the tips. Secondly, following Pio *et al.*'s (2014) approach, we sequentially pruned species from each phylogenetic tree according to the CSH values. The species predicted to have the largest loss in area of suitable habitat (lowest CSH) was dropped from the tree in the first pruning event, the two species predicted to have the largest and second largest losses were dropped from the tree in the second pruning event and so on. After each pruning event, the remaining PDs were calculated and compared to the random remaining PD generated by 99 replicates of pruning events when the same number of randomly selected species were dropped.

Results

Among the four scenarios of projected climate and land-use change in the 2080s, an average of 51% (range from 45–61%) of North American plants are projected to experience northward shifts in suitable habitats (Fig. 1), including 1608 species (22%) with north-west movements, 1098 species (15%) with northward movements and 1040 species (14%) with north-east movements. Of the 3411 species with northward range shifts under the A1b CGCM3 scenario by the 2080s, 1233 species (17% of total species number) would require migration rates of 10 km per decade to keep pace with their current suitable conditions, while 783 species (10%) would require the movements of >40 km per decade. Under the B1 CGCM3 scenario, results were less pessimistic with 1586 species (21%) needing migration rates of <10 km per decade and 332 species (4%) requiring migration rates of >40 km per decade.

Under the A1b emission scenario for the 2080s, we projected that 2037 species (27% of total species number) would experience >80% loss of suitable range conditions, 2419 species (32%) would have little directional change (−20% to 20%) and 92 species (1·2%) would greatly expand their suitable range conditions (>80%) (Fig. 2a). Similarly, >1800 species (24%) could lose 90% of their current suitable conditions under the A1b scenario by the 2080s (Fig. 2b). When considering a more conservative 50% gain or loss threshold, 3008 species would experience >50% range loss and 233 species would have >50% range expansion (Fig. 2a).

Surprisingly, species' sensitivity to the joint effects of climate and land-use change was not correlated with species rarity (Figs S2–S4). Closely related species tended to have similar expected responses to environmental change, indicating some degree of phylogenetic niche conservatism, but the strength of the phylogenetic signal was weak (Abouheif's *Cmean* = 0·34, *P*-value <0·01; Blomberg's *K* = 0·11, *P*-value = 0·02). Evolutionarily distinct species also tended to have greater reductions in suitable

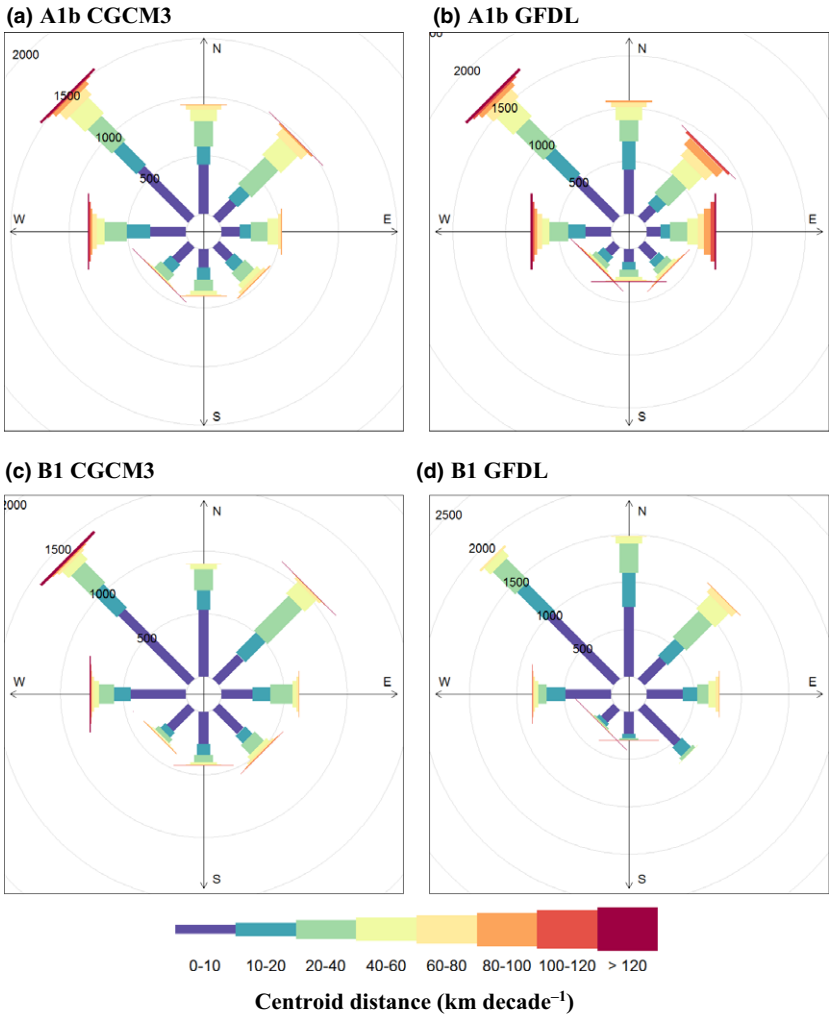

Fig. 1. Centroid changes in direction and distance of species range between current and projected distributions for the 2080s (2071–2100) under two greenhouse gas emission scenarios (A1b and B1) and two climate models (CGCM3 and GFDL): (a) A1b CGCM3, (b) A1b GFDL, (c) B1 CGCM3, and (d) B1 GFDL. The centroid change of each species was assigned to one of eight directions. Different colours in the figures represent the distance (magnitude) of species range shifts, while the length of each colour bar indicates the number of species at that projected range shift distance interval. [Colour figure can be viewed at wileyonlinelibrary.com]

range (environmental space) compared with species belonging to younger lineages, although again this pattern was weak (Table S2).

By comparing the changes in the proportions of stable species between current and projected distributions, many species were projected to have stable distributions in Canada and in the northern USA (high latitudes), while few species were estimated to be stable in Mexico and the southern USA (low latitudes) (Fig. 3a). Gains in species were expected in the north-eastern USA and Canada and parts of Texas and the Midwestern USA while being low in northern Mexico, California and the southern USA (Fig. 3b). Patterns in species loss appeared to be inversely related to stable species patterns with losses being high in Mexico and the southern USA (Fig. 3c). Finally, the patterns in species turnover suggested low turnover along the west coast, Rocky Mountains, Maritime (eastern) Canada and in the high Arctic, while turnover was predicted to be high for Mexico, Texas and the eastern boreal forests of Canada (Fig. 3d). These general patterns were also supported by the comparisons along a latitudinal gradient (Figs S5, S6).

Predicted phylogenetic diversity (PD) under future climate and land-use change was significantly lower than expected by random species loss (Fig. 4a,b). Predicted PDs calculated by sequential pruning of species with high extinction risk were also much lower than PDs calculated by randomly pruning the same number of species (Fig. 4c,d).

Discussion

Our study suggests that the distribution of suitable conditions for North American plant species will rapidly change in the 21st century (IPCC 2014; Melillo, Richmond & Yohe 2014; Warren & Lemmen 2014). We predicted a 20 : 1 loss to gain in species suitable habitat in North America with approximately 2000 species losing >80% of their current suitable habitats (1800 at >90% loss), while nearly 100 species will experience >80% expansion in suitable habitats. These results are consistent with previous studies for birds, mammals and amphibians across North and South America (Lawler *et al.* 2009) and for birds, mammals and butterflies in Mexico (Peterson *et al.* 2002). A recent meta-analysis of 131 studies examining biodiversity threats from climate change suggested that nearly one in six species may go extinct under current policies of carbon emissions (Urban 2015). Previous work on plants in Europe (Thuiller

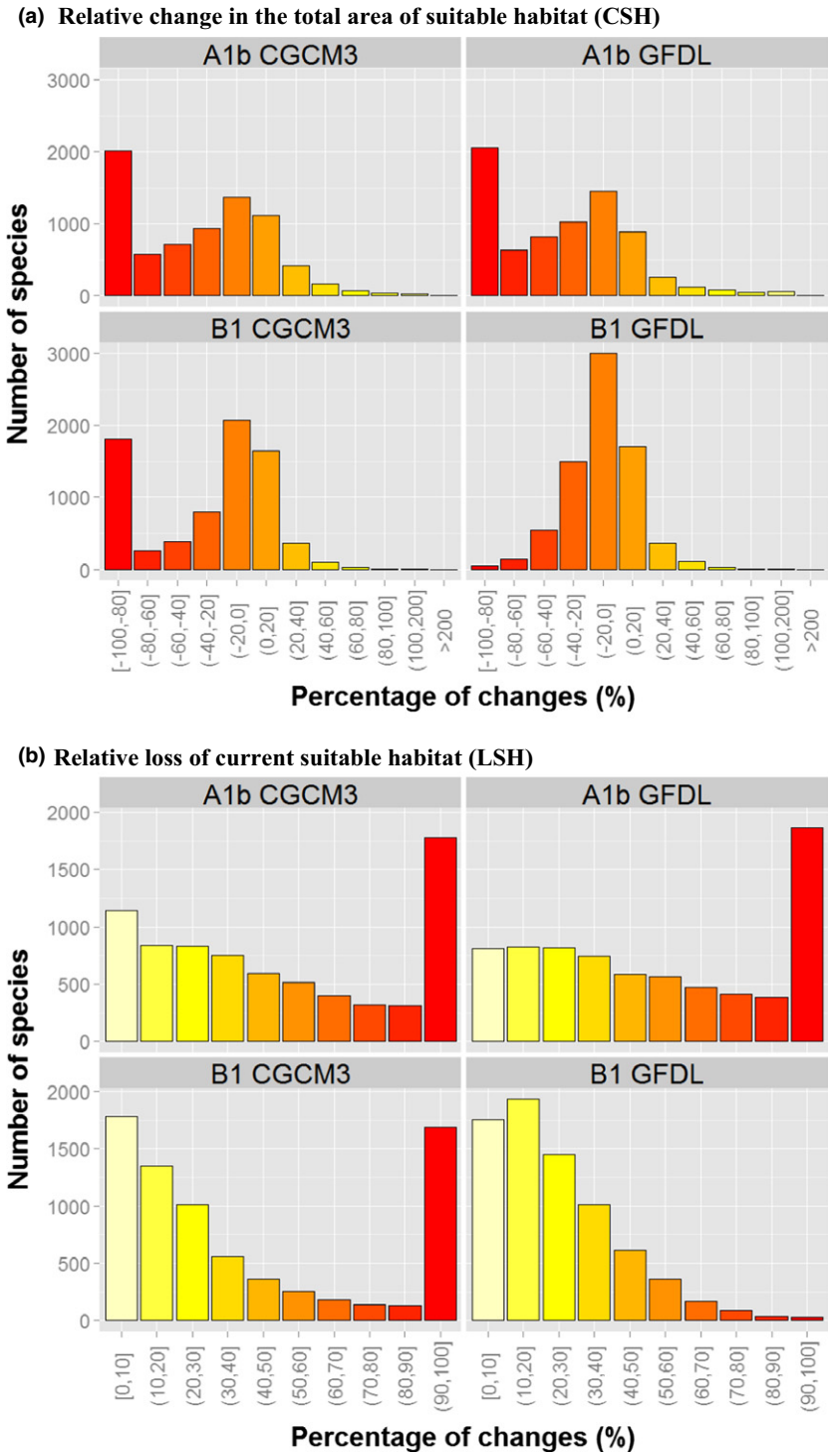

Fig. 2. Species' vulnerability to climate and land-use change by the 2080s (2071–2100) with two greenhouse gas emission scenarios and two climate models. (a) Upper panel represents change in the total area of suitable habitats (CSH, ranging from -100% to >100%). (b) Lower panel represents loss in current suitable habitats (LSH, ranging from 0% to 100%). [Colour figure can be viewed at wileyonlinelibrary.com]

et al. 2005, 2011), North American tree species (Mckenney *et al*. 2007) and Californian plant species (Kelly & Goulden 2008; Loarie *et al*. 2008) support these findings. In fact, compared with birds and large mammals, most plant species have much lower dispersal (Cunze, Heydel & Tackenberg 2013), making them more difficult to track in rapidly changing environments (Svenning & Sandel 2013).

For North America, we found that the largest loss in species richness is expected for low latitudes, while the largest gains are expected at higher latitudes. These results are expected given prior patterns during the Last Glacial Maximum (Prentice, Bartlein & Webb 1991; Clark *et al*. 1998). This northward shift will increase species richness in northern regions, while southern regions will be at greater risk of decline in species richness if species from Central and South America fail to immigrate into the region. However, such immigration would likely be at low rates due to the narrow and highly heterogeneous geography of Central America. One possible explanation of higher losses of species at low latitudes is that there are

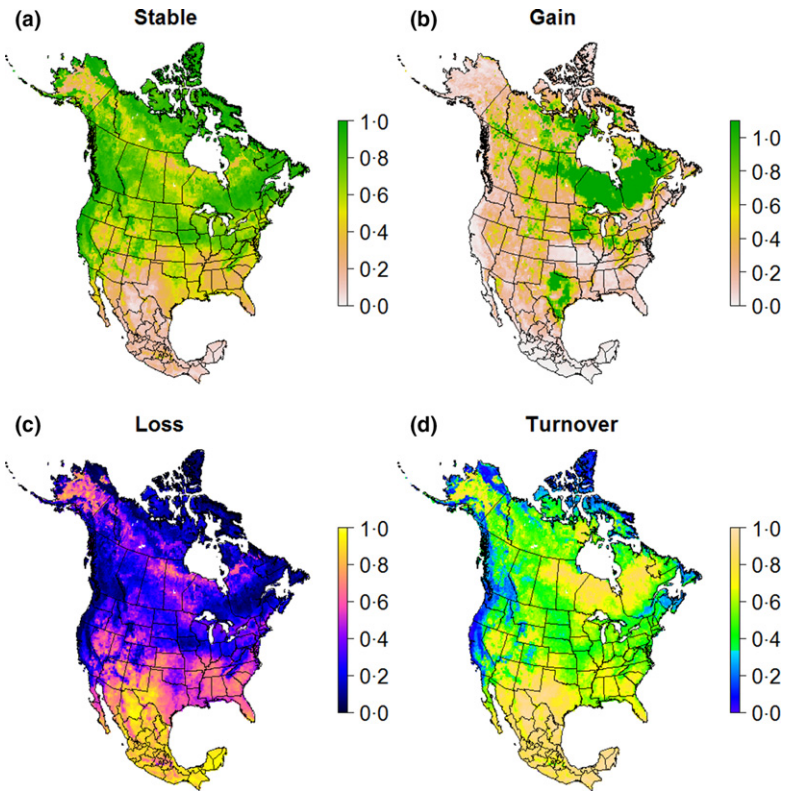

Fig. 3. Proportions of (a) stable, (b) gain, (c) loss and (d) turnover of plant species between current and projected distributions in the 2080s under A1b greenhouse gas emissions scenarios (GCM: CGCM3). Stable, gain and loss correspond to areas where species are predicted to remain, gain and lose suitable conditions, respectively. Species turnover was simply defined as the relative change in species composition in each grid cell. [Colour figure can be viewed at wileyonlinelibrary.com]

more species at low latitudes with narrow distributions/ranges (e.g. endemic, threatened or endangered species) (Urban 2015).

Adding evolutionary history into species range shift studies provides more insight into understanding species vulnerability and extinction risk (Thomas *et al.* 2001; Vamosi & Wilson 2008; Lavergne *et al.* 2010; Thuiller *et al.* 2011). Interestingly, the significant signal of non-random extinctions found here for North America flora contrasts with several previous studies. Both Thuiller *et al.* (2011) for 1760 European plants and animals and Pio *et al.* (2014) for four plant and animal groups in southern Africa found that expected losses in phylogenetic diversity from climate change did not differ from a random expectation. In other words, species sensitive to projected environmental change were randomly distributed across the tree of life. In contrast, our results indicate that evolutionarily distinct species in North America tend to be more sensitive than extant species, suggesting that there will be a disproportionate loss of evolutionary history (Purvis *et al.* 2000; Vamosi & Vamosi 2008; Eiserhardt *et al.* 2015). Species most at risk of decline in North America had significantly smaller range sizes (e.g. the average range size of the 10 most evolutionarily distinct species is less than one-third the range size of the next ten species), and thus, they are more sensitive to rapid environmental change (Purvis *et al.* 2000; Thomas *et al.* 2004; Vamosi & Wilson 2008). Future environmental change would place other species with small ranges (many endemic, threatened or endangered species) in greater danger (Urban 2015). These small-range species were more likely to be underrepresented in this analysis given that the data required for modelling species distributions tended to emphasize more common species. Our analyses may therefore underestimate the consequences of future climate and land-use change on the plant tree of life.

Although our analysis addressed some shortcomings of previous studies, our projections are subject to limitations common to SDM (Franklin 2009). Although our study included a large number (7465) of the North American plant species, there were taxonomic and phylogenetic biases in the data. For example, there were 177 genera (9% of total number of genera) without the detailed genus-level phylogenies, which may lead to some biases of extinction risk analysis across the tree of life. Having a more complete coverage of a flora at the continental scale will allow for greater insight into the spatial structure of the flora and the ability to highlight hotspots and cold-spots of species richness, as well as the patterns of phylogenetic diversity and endemism. Another limitation is the uncertainty in the SDMs. We used an ensemble-forecast approach to combine predictions from multiple SDMs with a restricted maximum dispersal rate of 20 km per decade to reduce overpredictions in SDMs (Kremen *et al.* 2008; Chen *et al.* 2011; IPCC 2014) across two global change models and two socioeconomic scenarios combined with a land-use change model. Although such an approach provides good representation of the uncertainty given the models and scenarios (Thuiller *et al.* 2005, 2011), numerous uncertainties remain, such as the potential effects of species interactions and species-specific range shifts (Franklin 2009; Hille Ris Lambers 2015). In

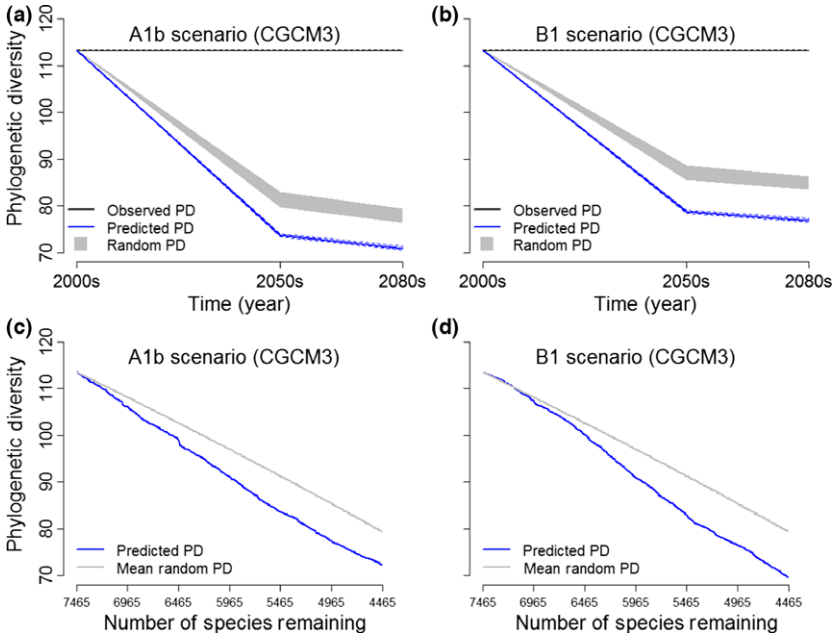

Fig. 4. Effects of climate and land-use change on the tree of life for North American plants. (a, b) Changes in total phylogenetic diversity (PD) compared with scenarios of random extinction under A1b and B1 greenhouse gas emissions scenarios (GCM: CGCM3). Change in the total area of suitable habitats (CSH) was used as a surrogate of survival probability for each species. Black solid and dashed lines show the median, maximum and minimum current PD across the 100 estimated phylogenies. Blue solid and dashed lines represent the median, maximum and minimum predicted PD due to changes in species range across the 100 trees. The grey area is the quantile range of null model expected PD by randomizing extinction probabilities across the tips. (c, d) The comparison of predicted versus random remaining PD. Predicted PD was calculated by sequentially pruning each phylogenetic tree by order of increasing CSH (low values of CSH indicate high extinction risk). Mean random PD was calculated by randomly pruning the same number of species with the analysis of predicted PD. [Colour figure can be viewed at wileyonlinelibrary.com]

addition, the shortage of high-quality species occurrence data and high-resolution climate and land-use data could also increase the uncertainty of SDM projections (Urban 2015). Building more mechanistic models of biodiversity is an area of active research (Thuiller *et al.* 2013), but we are still far from being able to build mechanistic models of species distributions that include interactions for over 7000 species. A few comparisons between mechanistic models of species distribution suggest that SDMs do a reasonable job in predicting the long-term range shift of species. In other words, they may not give the exact answer for a specific time period (i.e. 2080 horizon), but the projected trends are likely to be realistic in the long term (Hijmans & Graham 2006; Kearney, Wintle & Porter 2010).

In conclusion, we predicted major shifts of plant species distribution across the North American continent with changes likely to be non-random across the tree of life. Notably, evolutionarily distinct species were more sensitive to future climate and land-use change than other species, highlighting a disproportionate risk of loss in phylogenetic diversity [similar to past floristic losses due to late Cenozoic climate change (Eiserhardt *et al.* 2015)]. Our study highlights the importance of integrating evolutionary history into species distribution modelling and assessments of extinction risk to better inform biodiversity conservation and management. The marriage of phylogenetic diversity, SDMs and applied conservation practices holds promise for efficiently and strategically achieving the Aichi Targets under Convention on Biological Diversity (CBD) for 2020 (CBD 2015) and maximizing biodiversity protection in a changing future (Winter, Devictor & Schweiger 2013). Importantly, the identified phylogenetically non-random climate and land-use extinction risk for North American plant species suggests that conservation planning needs to more directly focus on evolutionarily distinct species to avoid disproportionate losses of phylogenetic diversity. Furthermore, a recent study by Jenkins *et al.* (2015) has shown that protected areas in the USA are not well located to broadly represent the diversity of terrestrial vertebrates, freshwater fish and tree species. Our continent-level forecasts can be used to further identify areas to be prioritized for conservation to minimize species and phylogenetic losses from climate and land-use changes. In addition, our projections of over 7000 plant species distributions could be used to improve the future assessments of the current conservation status of biodiversity in North America.

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Data accessibility

Data on species range changes between current and projected distributions in the 2050s and 2080s are available as online Supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. The performance of species distribution models for each of 7465 North American seed plant species.

Fig. S2. Species' vulnerability to climate and land-use change with respect to their rarity status.

Fig. S3. Species' vulnerability to climate and land-use change with respect to their status in the IUCN (International Union for Conservation of Nature) Red List.

Fig. S4. Species' vulnerability to climate and land-use change with respect to their rarity status in NatureServe data base.

Fig. S5. Absolute predicted change in species richness along a latitudinal gradient between current and projected distributions in the 2080s for the four combinations of future emission scenarios, land use and climate models.

Fig. S6. Absolute predicted change in species richness along a latitudinal gradient for North America north of Mexico between current and projected distributions in the 2080s for the four combinations of future emission scenarios, land use and climate models.

Table S1. Family-level summary of species richness, total number of occurrence records, averaged species distribution model performances (TSS: true skill statistics) and averaged suitable habitat changes (CSH: percentage change in the total area of suitable habitats; LSH: percentage loss in current suitable habitats) between current and the 2080s under A1b scenario (GCM: CGCM3).

Table S2. Pearson correlation between species' evolutionary distinctiveness (ED) and predicted species' change in suitable areas for the different time periods, the two emission scenarios and two climate models.

Appendix S1. Criteria used for data cleaning on species names and geographic occurrences.

Appendix S2. Data on species range changes between current and projected distributions in the 2050s and 2080s.