



Gains and losses of plant species and phylogenetic diversity for a northern high-latitude region

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ABSTRACT

Aim Forecasting potential patterns in species' distributions and diversity under climate change is crucial for biodiversity conservation. Although high-latitude regions are expected to experience some of the greatest increases in temperature due to global warming, little is known on how individual responses in species will affect patterns in phylogenetic diversity (PD).

Location Alberta, Canada.

Methods We used 160,589 occurrence records for 1541 species of seed plants in Alberta (nearly 90% of the province's seed flora) and ensemble niche models to project current and future suitable habitats. We then examined climate change vulnerability of individual species and the potential impacts of climate change on species richness, PD and both taxonomic and phylogenetic endemism (PE). We also assessed whether predicted losses of PD were distributed randomly across the plant tree of life.

Results We found that 368 species (24%) may lose on average > 80% of their current suitable climates (habitats), while 539 species (35%) were projected to more than double their current suitable range. Both species richness and PD were predicted to increase in most areas, except for the species-rich Rocky Mountains, which are predicted to experience future declines. Maps of taxonomic and PE identified several regions with high conservation value and climate change threat suggesting priorities for conservation and climate change adaptation. Overall, a non-random extinction risk was found for Alberta's flora, demonstrating potential future impacts of climate change on the loss of evolutionary history.

Main conclusions Our analyses suggest that climate change will have asymmetrical effects on the distribution of Alberta's plant diversity and endemism and a non-random extinction risk of the current state of species evolutionary history. Our results provide practical guidance for biodiversity conservation and management in this region by prioritizing species' vulnerabilities and places with higher taxonomic or evolutionary risk due to future climate change.

Keywords

climate refugia, ecological niche modelling, ensemble forecast, evolutionary diversity, extinction risk, range shift.

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INTRODUCTION

Climate change trends over the past century have affected a wide number of ecosystems, and these effects are projected to increase in the coming decades (Millennium Ecosystem

Assessment, 2005; IPCC, 2014). Despite the remarkable number of studies on the consequences of climate change on biodiversity (Pimm *et al.*, 2014; Lenoir & Svenning, 2015), most studies have focused on changes in species ranges and species richness (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Jetz

et al., 2007; Franklin, 2009). Rarely have climate change risk assessments considered other facets of biodiversity (but see Thuiller *et al.*, 2011, 2014; Pio *et al.*, 2014). In particular, these assessments rarely consider evolutionary measures of biodiversity, despite their long history of recognition (Darwin, 1859; Purvis *et al.*, 2000).

Loss of a more distinct species, with respect to its evolutionary history, results in a greater total loss of biodiversity than loss of a non-distinct species with many close relatives (Purvis *et al.*, 2000). Evolutionary distinct species should therefore be of greater conservation priority (Isaac *et al.*, 2007; Winter *et al.*, 2013) as disproportionate losses of species' evolutionary or phylogenetic diversity (PD) could lead to both non-random extinction across lineages and more homogenous landscapes (i.e. more similar species across landscapes) (Purvis *et al.*, 2000). How climate change will influence loss of PD remains uncertain (Vamosi & Wilson, 2008; Thuiller *et al.*, 2011; Pio *et al.*, 2014) and appears to depend on the methods and data used. Vamosi & Wilson (2008) reported disproportionate projected losses of PD for plants by using threat categories from the IUCN Red List. In contrast, Thuiller *et al.* (2011) projected current and future distributions for 1280 plant, 340 bird and 140 mammal species in Europe and predicted a homogenization of PD across the region. Loss of PD was not higher, however, than expected by null models. Likewise, Pio *et al.* (2014) used a similar approach in southern Africa to examine changes in PD for two plant families (314 species), one mammal order (50 species) and one insect genus (26 species), concluding that the effects of climate change would be random with respect to phylogenetic species extinctions. These assessments using species distribution models contradict previous studies using simple IUCN threat status assessments (Purvis *et al.*, 2000; Vamosi & Wilson, 2008). Further studies are therefore needed to better understand potential consequences of

climate change on different facets of biodiversity and in particular PD.

Northern high-latitude regions are expected to experience some of the greatest increases in temperature in the near future (IPCC, 2014). Western Canada's boreal zone has already experienced a 2°C increase in mean annual temperature from 1950 to 2003 (Lemprière *et al.*, 2008) and is projected to increase an additional 4–5°C by 2100 (Price *et al.*, 2011). Climate warming in this region is expected to increase the frequency of wildfires (Flannigan *et al.*, 2005), insect outbreaks (e.g. mountain pine beetle, Kurz *et al.*, 2008) and regional droughts (Hogg *et al.*, 2008; Allen *et al.*, 2010). It is timely to therefore study the current and future community structure, function, biodiversity and dynamics of high-latitude regions with respect to current and future climates.

In this study, we provide a comprehensive evaluation of predicted impacts of climate change on plant richness, PD and both taxonomic and phylogenetic endemism (PE) using a database of 1541 seed plant species in Alberta, Canada. Alberta presents one of the best opportunities for studying the impacts of climate change on plant species and PD due to the nearly complete digitization of herbarium collections and other rich sources of distributional data across a large region (66.2 million hectares) composed of a variety of environments from dry grasslands to alpine habitats to northern boreal forests (Fig. 1, Table 1). Here, we used average projections from an ensemble of ecological niche models (ENMs) to predict climatic habitat suitability for each species under current and future climates at a 4-km resolution. Specifically, our objectives here were to (1) map current potential distributions of suitable habitat for each plant species and examine their potential range shifts under climate change; (2) assess the vulnerability of each species to climate change; (3) map taxonomic diversity, PD and endemism to evaluate their changes between current and future climates, including

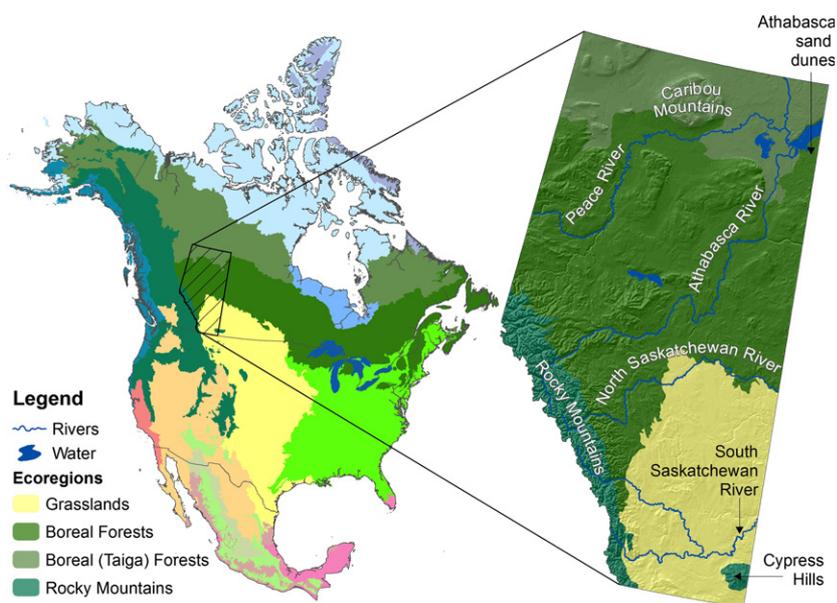


Figure 1 Location of the study area in the province of Alberta, Canada (49°–60°N, 110°–120°W). Total area of this province is 66.2 million hectares. Four ecoregions of Alberta, which were classified by climate and biophysical information, are shown in different colours.

Table 1 Data sources of species occurrence data on Alberta seed plant species.

Data Source	Description	Number of species occurrence	Number of seed plant species
Alberta Conservation Information Management System (ACIMS)	A comprehensive database of Alberta biodiversity information (ACIMS, 2013)	8736	372
Ecological Monitoring Committee for the Lower Athabasca (EMCLA)	Includes 355 plots collected by EMCLA (http://www.emcla.ca) in 2012–2013 (Zhang <i>et al.</i> , 2014a)	15,275	457
Permanent sampling plots (PSPs)	Includes 2392 plots collected by Alberta Environment and Sustainable Resource Development, Weyerhaeuser Canada and West Fraser Mill Ltd. (Zhang <i>et al.</i> , 2014b, 2015)	7989	14
Alberta Biodiversity Monitoring Institute (ABMI)	Includes 667 ABMI (http://www.abmi.ca) sites collected in 2003–2012 across the whole province (Zhang <i>et al.</i> , 2014c)	38,408	1009
Global Biodiversity Information Facility (GBIF)	GBIF (http://www.gbif.org) is a comprehensive database that currently holds over 500 million records of species occurrences (Yesson <i>et al.</i> , 2007). We downloaded seed plant records for Alberta region for the current study	27,602	1420
National Park Plots	Includes 4090 plots established in 1977–1979 within Banff National Park, Kootenay National Park, Jasper National Park and Yoho National Park (Nielsen <i>et al.</i> , 2003)	57,550	622
Willmore Wilderness Plots	Includes 149 plots collected in the Willmore Wilderness Area in 2001–2003 (Gould, 2007) and 2009–2010 (Joyce Gould, Alberta Parks, unpublished)	249	13
Foothills Plots	Includes 2849 plots sampled in 2001–2008 in west-central Alberta for grizzly bear habitat assessments (Nielsen <i>et al.</i> , 2010)	4780	13
Total		160,589	1541

identification of climate refugia; (4) evaluate whether species extinctions (extirpations) due to climate change will be random with respect to a phylogenetic tree; and (5) assess how these outcomes could affect the biodiversity of Alberta's landscapes in the future.

METHODS

Study area

The study area was the province of Alberta, Canada (49°–60°N, 110°–120°W), representing an area of 66.2 million hectares (Fig. 1). Alberta encompasses six natural regions: Boreal, Foothills, Rocky Mountains, Canadian Shield, Parkland and Grasslands (Alberta Natural Regions Committee, 2006). These regions have short summers, and long and cold winters. Mean annual temperature ranges from –2.6°C in the Canadian Shield to 4.0°C in the Grasslands. Mean warmest monthly temperature ranges from 11.0°C in the Rocky Mountains to 17.8°C in the Grasslands, and mean coldest monthly temperature (January) ranges from –25.1°C in the Canadian Shield to –11.7°C in the Grasslands. Mean annual precipitation ranges from 374 mm in the Grasslands to *c.* 800 mm in the Rocky Mountains. Elevation ranges from *c.* 150 m near the Alberta–Northwest Territories border in the north to over 3600 m in the Rocky Mountains in the south-west. This

variation in climate and topography results in a wide range of climates and vegetation types.

Species occurrence data

We combined seed plant species occurrence data from multiple data sources, including Alberta Conservation Information Management System (ACIMS), Ecological Monitoring Committee for the Lower Athabasca (EMCLA), Alberta Biodiversity Monitoring Institute (ABMI) and others (see Table 1 for the detailed description). To reduce potential errors in species' names and geographic locations of occurrence data, we used eight criteria to improve data quality (Appendix S1). Finally, we selected 160,589 occurrence records (Table 1) to model ecological niches for a total of 1541 species of seed plants from 483 genera and 90 families (Table S1). Among these species, 1519 species are angiosperms and 22 species are gymnosperms, representing nearly 90% of Alberta's seed flora (Moss, 1983). In addition, 119 (*c.* 8%) of 1519 species are non-native (ACIMS, 2013). Considering possible influences of non-native species on community assembly (Chai *et al.*, 2014), we included them into the current analysis.

Environmental variables

Current climate variables for Alberta at a 4-km spatial resolution were based on the ClimateNA data set for the baseline

period of 1961–1990 (Stralberg *et al.*, 2015; <http://tinyurl.com/ClimateNA>), comprising 20 biologically relevant variables (Hamann *et al.*, 2013).

Climate variables in the 2050s (2041–2070) and 2080s (2071–2100) were also based on ClimateNA. Two general circulation models (GCMs), Coupled Global Climate Model (CGCM, version 3.1) and Geophysical Fluid Dynamics Laboratory's coupled climate model (GFDL-CM, version 2.1), have been recommended for North American projections (Stralberg *et al.*, 2015) and were selected here. For each GCM, we included two emissions scenarios, A1B and B1. A1B scenario represents a future world with maximum energy requirements, and the B1 scenario represents a convergent world with lower energy requirements (Nakicenovic, 2000). Although there are two other scenarios available in the A1 family, we selected A1B because it represents a balanced emphasis on all energy sources.

To reduce multicollinearity, Pearson's correlation and variance inflation factor (VIF) were used for variable selection (Marquardt, 1970). Variables with Pearson's correlation coefficients $> |0.70|$ were considered highly correlated. A VIF > 5 was used to indicate collinearity.

Predicting distribution shifts under climate change

We used five modelling algorithms to model potential suitable habitat for each species, including generalized additive models (GAM; Hastie & Tibshirani, 1990), boosted regression trees (BRT; Friedman, 2001), random forests (RF; Breiman, 2001), maximum entropy (Maxent; Phillips *et al.*, 2006) and multiple adaptive regression splines (MARS; Friedman, 2001). Models were calibrated for the baseline period using a random sample of 70% of the initial data, while predictive accuracy of the models was evaluated with the remaining 30% of data using the true skill statistic (TSS) (Allouche *et al.*, 2006). This *k*-fold cross-validation procedure (Boyce *et al.*, 2002) was repeated five times for species with ≥ 100 occurrence records, and 10 times for those with < 100 occurrence records (Barbet-Massin *et al.*, 2012). The repetitions ensure that model evaluation is not a function of a specific sampling split. All calibrated models were then projected under current and future conditions at a 4-km resolution. In addition, considering the possible influence of covering only parts of the whole ranges for some species, we used a climate-matching approach to evaluate to which extent Alberta's climate matches with other regions in North America north of Mexico (Appendix S1, Fig. S1). We also compared predicted range sizes of ENMs under current climate using data from Alberta-only and from Alberta and its two-degree neighbour regions, and found a high correlation (Pearson's correlation coefficient = 0.87) between these two predicted ranges of 654 selected species (Appendix S1, Fig. S2). We were thus confident that our estimated niches were relevant and could be used for projecting under climate change.

To summarize model predictions in a meaningful integrated projection, an ensemble of forecasts of ENMs was

obtained for each species for each scenario and GCM (Araújo & New, 2007) (Appendix S1). Models and the ensemble forecasting procedure were performed within the BIOMOD2 platform (Thuiller, 2003; Thuiller *et al.*, 2009) in R language (R Core Team, 2014). All species distribution maps are available on the 'Alberta Species Conservation Atlas' website: <http://www.ace-lab.ca/index.php?page=asca>.

Measuring species' vulnerability

To assess potential impacts of climate change on species ranges, we quantified species' vulnerability using two metrics for the ensemble projections (Thuiller *et al.*, 2011, 2014). The first metric assessed the relative change in total area of suitable habitat (CSH, ranging from -100 to > 100) using the equation: $CSH = (AREA_{Future} - AREA_{Current}) / AREA_{Current} \times 100$, where $AREA_{Future}$ is the area of future suitable habitats, and $AREA_{Current}$ is the area of current suitable habitats. This metric assumes perfect dispersal (migration) into new climate ranges. The second metric quantified the loss of current suitable habitat (LSH, ranging from 0 to 100) using the equation: $LSH = 100 - (Overlap(AREA_{Future}, AREA_{Current}) / AREA_{Current} \times 100)$. This metric provided an indication of the risk of local extinction as it does not consider migration into new ranges (i.e. zero dispersal assumption). A species losing 100% of its current suitable habitat is at high risk of extirpation even if it is projected to gain new suitable habitats elsewhere.

We also compared species' vulnerabilities to climate change based on growth form (forb/herb, graminoid, shrub and tree) and rarity. For rarity, we classified species into five categories using NatureServe subnational-level rankings – S1: critically imperilled, S2: imperilled, S3: vulnerable, S4: apparently secure and S5: secure (NatureServe, 2014). Rarity information was available in the NatureServe database for 95% of our focal species ($n = 1461$ species) (Table S1).

To detect the direction and distance of species range shifts under future conditions, we calculated the geographic centre of each species' range extent for current and future periods, and the directions and distances were measured based on the changes between current and future centroids. This analysis was performed using 'gCentroid' function in the R package 'rgeos' (<https://r-forge.r-project.org/projects/rgeos>).

Measures of taxonomic and phylogenetic diversity and endemism

We created maps representing taxonomic and PD from the binary models of potentially suitable habitat (distribution) for all 1541 plant species for both current and future time periods. For taxonomic diversity, we mapped species richness, change in species richness, species loss (L), species gain (G) and species turnover (T) for each emission scenario and GCM. Species turnover (T) was defined as the relative change of species composition in each grid (i) and was calculated using the equation: $T_i = (L_i + G_i) / (SR_i + G_i)$, where

SR is the current species richness in grid i . We used the corrected weighted endemism (CWE) (Crisp *et al.*, 2001) to assess taxonomic endemism within the context of Alberta. CWE is measured by summing the inverse of all species' range sizes (potentially suitable habitat) and dividing by local species richness. This index is therefore independent of total species richness (Crisp *et al.*, 2001). This does raise a question over the use of CWE specific to Alberta as we covered only a part of ranges for some species. The high correlation of predicted range sizes between data from Alberta-only and from Alberta and its neighbours (Appendix S1, Fig. S2) suggests that any potential biases in CWE would be small.

To measure PD and PE, we first adapted several previous studies (Thuiller *et al.*, 2011; Roquet *et al.*, 2013; Zanne *et al.*, 2014) to develop both genus- and species-level phylogenies (Appendix S1). Then, we evaluated PD using Faith's PD (Faith, 1992) and PE (Rosauer *et al.*, 2009). Faith's PD is the sum of all branch lengths of a phylogenetic tree representing all species with suitable habitat in each 4 km × 4 km grid. PE, which considers both Faith's PD and species' range size, is a measure of the amount of shared evolutionary history in each grid in relation to how widespread these species are geographically (Rosauer *et al.*, 2009). These analyses were performed using the R functions *phylo.div* and *phylo.endemism* developed by David Nipperess (available here: <http://davidnipperess.blogspot.com.au>). We calculated these two indices for each of the 100 phylogenetic trees and mapped the average of each index over the 100 trees.

Predicted effects of climate change on phylogenetic diversity

To assess whether estimated species' range shifts under future climates will lead to phylogenetic homogenization of Alberta's flora, we calculated two phylogenetic relatedness indices: net relatedness index (NRI) and nearest taxon index (NTI), respectively (Webb, 2000; Webb *et al.*, 2002). NRI is a standardized measure of mean pairwise phylogenetic distance among species in each sampled community. NTI is a standardized measure of mean nearest taxon phylogenetic distance. We used a null model in which species' names were randomly drawn 999 times from the regional phylogeny pool, holding species richness of each sample constant. Values of NRI and NTI close to zero indicate random phylogenetic structure, positive values indicate clustering, and negative values indicate overdispersion. These indices were calculated using the software PHYLOCOM 4.2 (Webb *et al.*, 2008) for each 4-km grid for each combination of time slice, GCM and emission scenario.

To test whether predicted losses of PD were random across the plant tree of life, two approaches were used. First, we used CSH as a surrogate for probability of extinction (extirpation) from Alberta and weighted the edge length of each of the 100 phylogenetic trees by the expected survival probabilities of each species under each time period and scenario (Thuiller *et al.*, 2011). Expected PD values were then

compared with those generated by the 99 replicates which considered CSH as random across the tips of each phylogenetic tree. Second, we sequentially pruned species from each phylogenetic tree according to the CSH values (Pio *et al.*, 2014). The species predicted to have the largest loss in area of suitable habitat (the lowest CSH) was dropped first from the tree in the first pruning event, and two species predicted to have the largest and second largest losses were dropped next from the tree in the second pruning event and so on. After each pruning event, remaining PD values were calculated and compared to random remaining PD values generated by 99 replicates of pruning events for which the same number of randomly selected species were dropped.

RESULTS

Species' range shifts in response to climate change

Assuming perfect dispersal, under the A1B CGCM3 scenario (Fig. 2a), 297 species (19% of the total species number) were predicted to lose > 80% of current suitable habitats by the 2080s, while 515 species (33%) were expected to more than double their current habitats. Under the A1B GFDL scenario, similar trends were found. Under the B1 scenario, predicted changes in species' ranges were less pessimistic than those under the A1B scenario. Without considering habitat expansion under the no dispersal scenario (Fig. 2b), approximately 300 species under the A1B scenario and 170 species under the B1 scenario are expected to lose > 90% of their current suitable habitats by the 2080s.

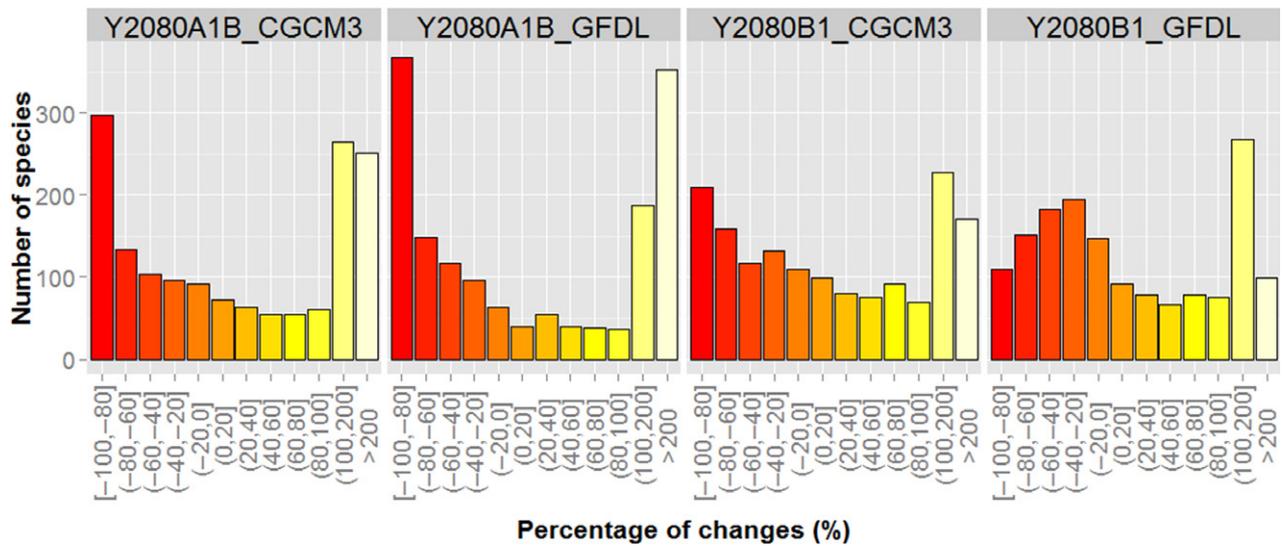
On average, forb and graminoid species were expected to experience considerable expansion of suitable habitat, and relatively low loss of current suitable habitat (Fig. S3). Tree and shrub species were predicted to respond to climate change differently, with some species (e.g. *Picea engelmannii* and *Pinus banksiana*) experiencing large contractions in habitat, while other species (e.g. *Salix farriae* and *Fraxinus pennsylvanica*) were predicted to have large expansions in suitable habitat. Contrary to what might be expected between rarity and climate change threats, no significant differences were found in changes of average range sizes (Fig. S4).

Direction and magnitude of species' range shifts varied greatly among species (Fig. 3). Under the A1B CGCM3 scenario for the 2080s, 1002 (65%) of 1541 species were expected to move their range centroids northward. Among these species, 716 species (72%) would need movement rates > 10 km per decade, including 237 species (24%) at a rate of 10–20 km per decade, and 479 species (48%) at a rate of > 20 km per decade.

Changes in taxonomic diversity and endemism

Under current climates, the Rocky Mountains have high plant richness, while the boreal forests are represented by low richness (Fig. 4a). Under future climate scenarios, species richness was predicted to increase in most regions with

(a) Relative change in total area of suitable habitat (CSH)



(b) Loss of current suitable habitat (LSH)

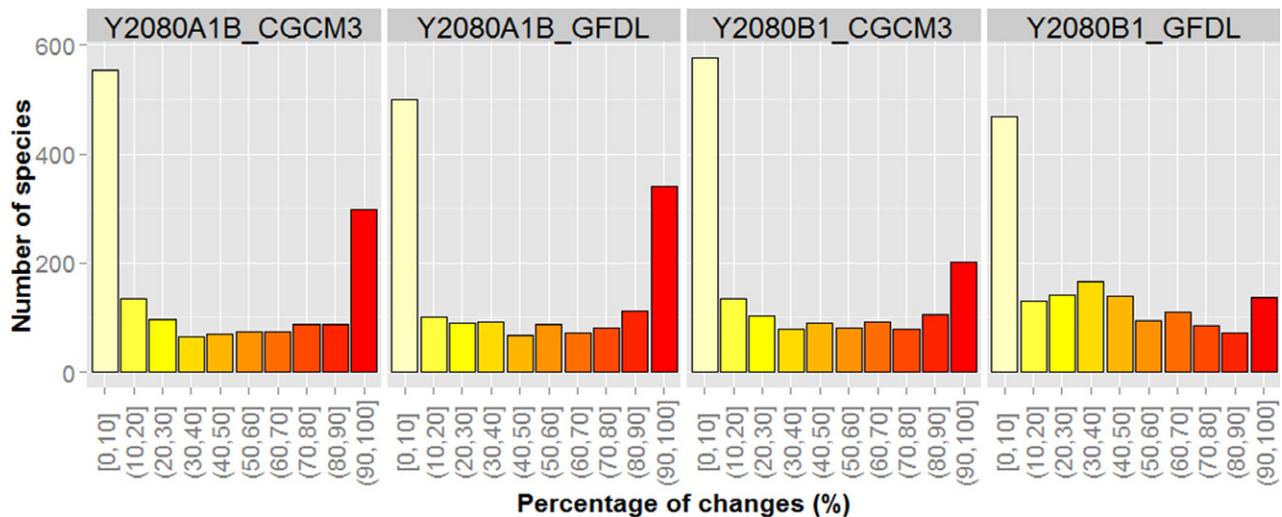


Figure 2 Species' vulnerability in response to climate change in 2080s (2071–2100). We used two indices, relative change of suitable habitat (CSH) and relative loss of current suitable habitat (LSH), to measure species' vulnerability using two greenhouse gas emission scenarios and two general circulation models (GCMs). For CSH, negative values represent projected losses in species habitat, while positive values represent projected gains in habitat (range expansion) assuming perfect dispersal. For LSH, assuming no dispersal, increasingly higher values indicate increasingly greater losses of current species' range.

the exception of the Rocky Mountains where a decline in richness is expected (Figs 4a & S5). By comparing areas of climate refugia defined by stable ranges of species (i.e. overlap between current and future suitable habitat; Fig. S6), we found that a large percentage of species had stable ranges in the Rocky Mountains, but this region is also predicted to gain fewer species resulting in the loss of more species compared to other regions.

Taxonomic endemism (CWE index) is currently highest in the Rocky Mountains in the south-west and the Athabasca sand dunes south of Lake Athabasca in the north-east, and moderate in some parts of the Grassland region in the south (Fig. 4b). Gains in taxonomic endemism were projected

under climate change in the Rocky Mountains, while two areas of Alberta were expected to see the largest losses in taxonomic endemism: the Athabasca sand dunes in north-east and the Cypress Hills in south-east Alberta (Fig. 4b). Despite increased richness for the northern boreal forest, taxonomic endemism is not predicted to increase with climate change, indicating that species gains in the region would be comprised of commonly distributed species.

Changes in phylogenetic diversity and endemism

Overall, patterns of PD and PE were similar to those of taxonomic diversity and endemism (Figs 4 & S7). Current areas

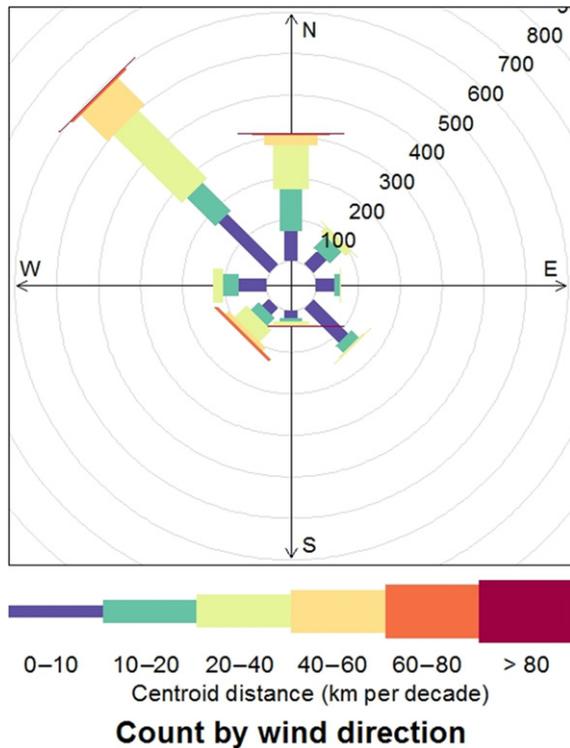


Figure 3 Centroid changes between current distributions of plant species and projected distributions under A1B emissions scenario [general circulation models (GCM): CGCM3] in the 2080s. Centroid changes of each species were assigned to one of eight migration directions. Different colours represent different distance magnitudes of species' range shifts, while the length of each colour bar indicates the number of species under its corresponding distance interval.

of high PD include the Rocky Mountains and to a lesser degree major river valleys that are directed to the north-east (e.g. Athabasca and North Saskatchewan Rivers), southern boreal forests in the east-central parts and southern Grasslands (Fig. 4c). Under future climates, plant richness is projected to increase for northern and central Alberta resulting in increased PD, especially for north-west and central parts (Fig. 4c). However, these gains in the northern and central parts were not expected to increase PE (Fig. 4d). Areas of high PE under future climates are predicted to again be greatest in the Rocky Mountains, accompanied by noticeable increases at moderate elevations in boreal forest areas such as the Caribou Mountains in north-central Alberta (Fig. 4d). PE is predicted to experience its greatest losses in the southern and northern parts of the Rocky Mountains and parts of the southern Grasslands, while predicted to increase in the central parts of the Rocky Mountains and the Caribou Mountains in the north-central boreal forests (Fig. 4d). When comparing phylogenetic relatedness between current and future climates, we predict that climate change will lead to a homogenization of evolutionary structure with significantly increased phylogenetic clumping in most parts of Alberta (Fig. S8).

Effects of climate change on the plant tree of life

By summarizing changes in species range across a family-specific phylogeny, we found that some families had higher extinction risk (Fig. 5). These high-risk families included those with singleton species, such as Myricaceae and Rhamnaceae. In particular, 9 of 16 pine species are predicted to lose > 80% of suitable habitats. In contrast, a few families with singleton species, such as Ruppiaceae, Lythraceae and Elatinaceae, are expected to experience substantial expansions in suitable habitat. Several families with high species richness, such as Poaceae (86 of 161 species) and Brassicaceae (45 of 92 species), are also expected to have > 80% expansion of habitats.

By comparing the expected total PD under climate change with scenarios of random extinction, we found that both approaches showed expected PD that was significantly different from random PD (Fig. 6), suggesting non-random species extinction across the tree of life.

DISCUSSION

Climate-induced range shifts

Here, we report a comprehensive evaluation of the predicted effects of climate change on a nearly complete collection of seed plant species and their distributions in Alberta. Using ensemble ENM techniques, we predict that plants in Alberta are expected to experience substantial spatial redistribution of suitable habitat by the end of this century. These findings are consistent with other studies of northern high-latitude environments, where global warming is expected to be more pronounced (Price *et al.*, 2013; IPCC, 2014). For example, Malcolm *et al.* (2002) predicted high species losses and required migration rates across the Northern Hemisphere, including Canada, Alaska and Russia, under a doubled- CO_2 climate change scenario using GCMs and global vegetation models. Likewise, Bergengren *et al.* (2011) found that Canada's prairie and boreal regions are expected to have major ecological changes by the end of this century using two ecological sensitivity metrics. Whereas these studies were based on coarse-scale vegetation distribution data or incomplete species distribution data, our work included 1541 species that account for nearly 90% of Alberta seed plant richness (Moss, 1983). Thus, we show a nearly entire picture of the current and future flora of Alberta at a relatively fine spatial scale, while providing more detail on how individual species would respond to climate change. Given the complex nature of plant community dynamics, it is challenging to predict how species assemblages will be affected by these changes (Peterson *et al.*, 2011). However, the present study offers additional insight into the implications of climate change for species' PD.

In Alberta, plant species are predicted to respond to climate change in a number of different ways. While a large number of mostly common species are expected to experience a northward expansion of suitable habitats, substantial losses are predicted for many other species, most of which

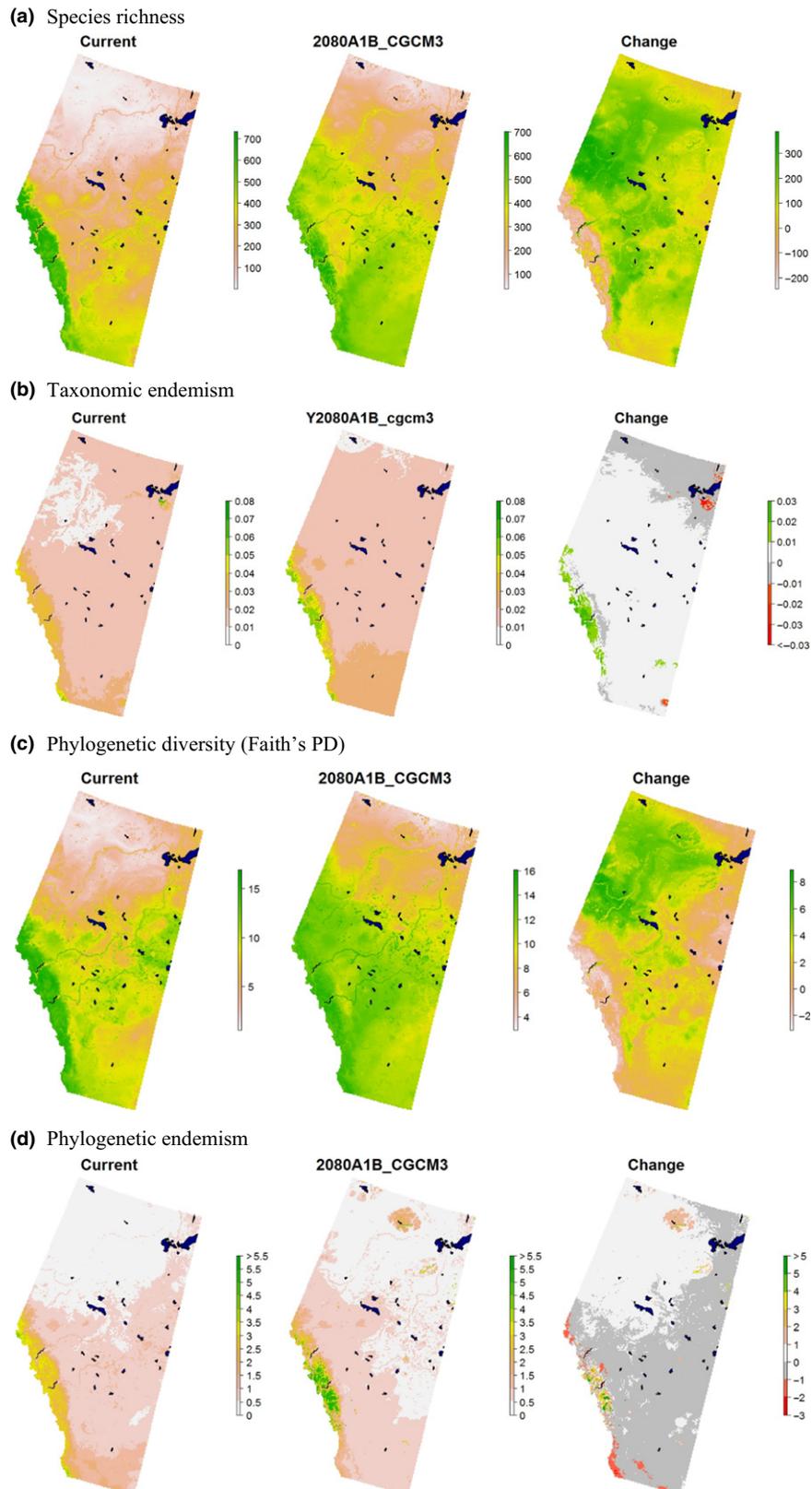


Figure 4 Species richness (a), taxonomic endemism (b), phylogenetic diversity (c) and phylogenetic endemism (d) at a 4-km resolution based on projected distributions under current conditions and the A1B emissions scenario [general circulation models (GCM): CGCM3] for the 2080s. Taxonomic endemism was measured by the corrected weighted endemism (CWE) index. Change is expressed as the absolute value of change between current and future periods. Blue areas represent large water bodies.

are rare to Alberta. This finding is consistent with previous studies of European plants (Thuiller *et al.*, 2005, 2011) and British Columbia tree species (Hamann & Wang, 2006). In Alberta, Barrow & Yu (2005) predicted that, under several climate change scenarios, mean annual temperature is expected to rise by 3–5°C by the 2050s, with degree-days above 5°C increasing by 30–50%, and dryness increasing by 20–30%. Increasing temperature and growing season length will clearly benefit some plant species, but also put some species that may not adapt to these new environments under greater pressure.

Species-specific responses to climate change also suggest that some species with limited dispersal ability may not be able to keep up with the changing climate (Chen *et al.*, 2011). According to our analyses, up to 479 (31%) of 1541 species need to move at least 20 km per decade to keep pace with projected change in suitable climates, which is unlikely to happen for most plant species (IPCC, 2014). In response to the projected loss of dispersal-limited species (e.g. *P. engelmannii*, *P. banksiana* and *Houstonia longifolia*), an

important climate change adaptation strategy is to translocate them to suitable habitats under future climates (Thomas, 2011). However, there are still many uncertainties and risks associated with such actions, and further assessments are needed if assisted translocation is to be considered (Minteer & Collins, 2010).

Impacts of climate change on taxonomic and phylogenetic diversity

In the northern high latitudes, species-specific range shifts in response to climate change will have considerable implications for biodiversity patterns. In Alberta, the Rocky Mountains harbour the highest plant richness. We projected a similar pattern for PD. This region is also a regional hotspot of endemic-like species as measured by both taxonomic and PE, while it is expected to lose more taxonomic and PD in the future than any other regions. Projected losses in taxonomic and PE in some parts of this region indicate that some endemic species could be at

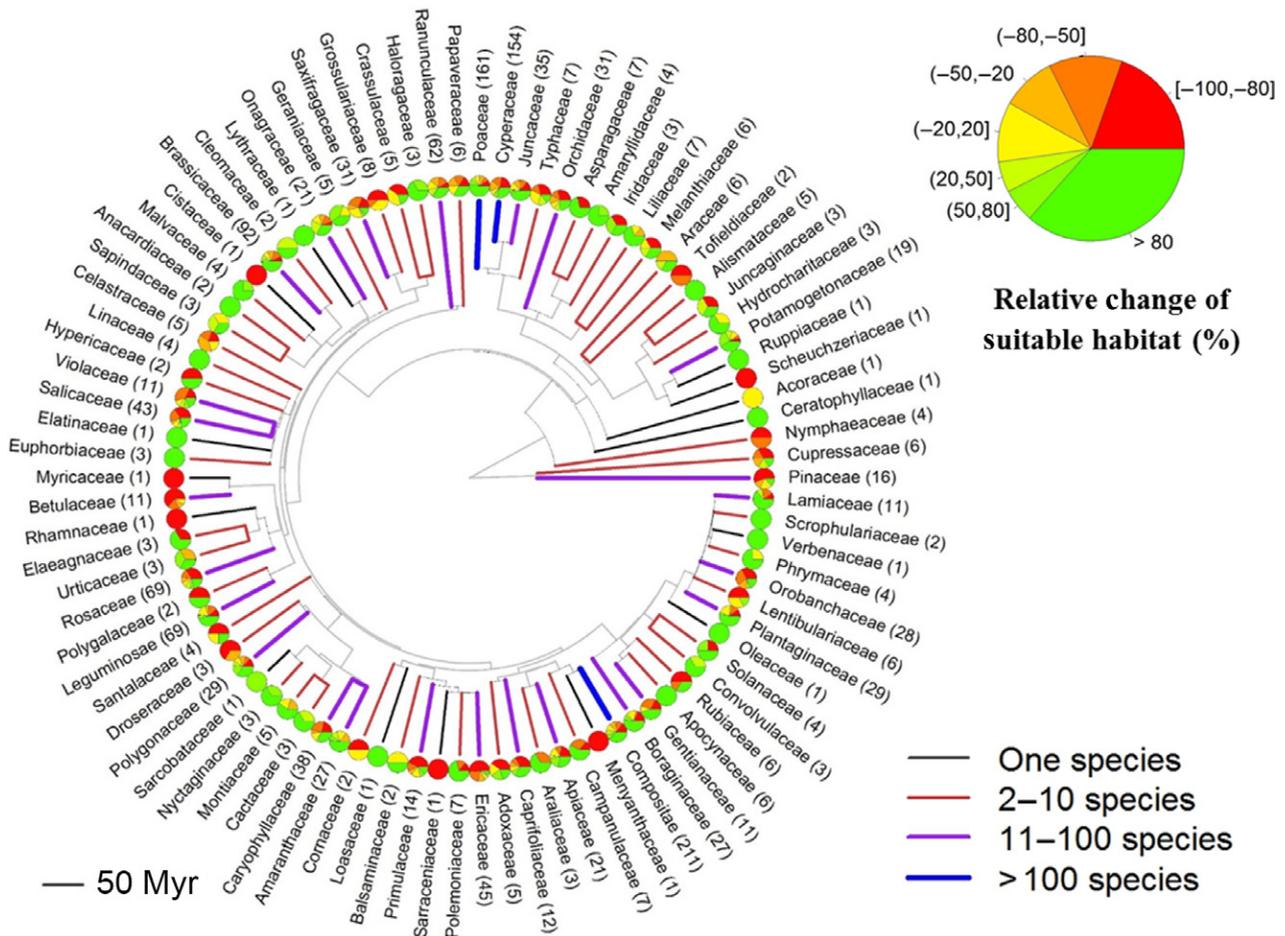


Figure 5 Projected changes of species composition in each plant family between current and 2080s (A1B CGCM3) conditions along the plant tree of life. Family names and corresponding number of species in each family were labelled around the phylogeny. Pie chart on the top right shows the percent of species relative to total species richness within each of seven different groups of habitat change. Pie charts located in the phylogeny show the percent of species relative to the total number of species in each family. Colours in these pie charts in the phylogeny correspond to the same values as the chart on the top right. Branch lengths are in millions of years (Myr).

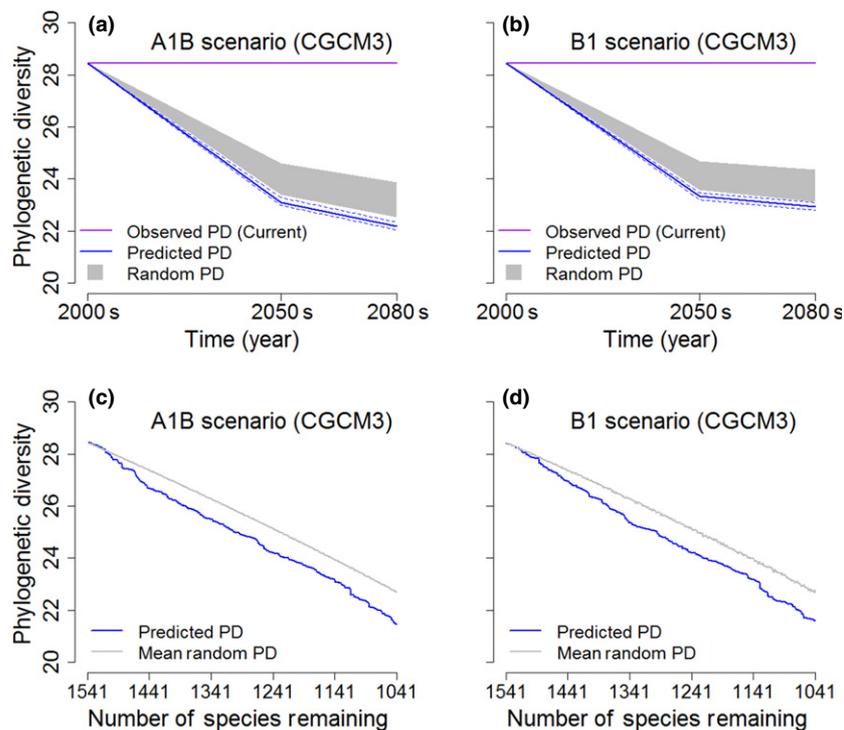


Figure 6 Effects of climate change on the plant tree of life. (a, b) Changes in total phylogenetic diversity (PD), comparing with scenarios of random extinction under A1B and B1 greenhouse gas emissions scenarios [general circulation model (GCM): CGCM3]. Change in total area of suitable habitats (CSH) was used as a surrogate of survival probability for each species. Purple solid lines show the median of current PD across the 100 estimated phylogenies. Blue solid and dashed lines represent the median, maximum and minimum predicted PD due to range change across the 100 trees. Grey area is the 5% and 95% 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 the order of the 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.

risk of extinction under climate change. In addition, Athabasca sand dunes located in the north-eastern Alberta and north-western Saskatchewan is a region with one of the highest rates of endemic plant species in Canada (Raup & Argus, 1982) and could face future losses of endemic species under climate change (Figs 1 & 4d). The isolated Cypress Hills in the south-eastern Alberta represent an island-like habitat of forests surrounded by grasslands that are expected to see future losses of its regional endemic-like species (Kulig, 1996). Our findings raise concern over the protection and mitigation of these regions against future climate change.

By measuring the degree of phylogenetic clumping in each 4-km grid cell under current and future climates, we found that phylogenetically similar species had higher probabilities of co-occurrence in each cell under future climate, leading to a homogenized landscape of evolutionary structure across Alberta. Thuiller *et al.* (2011) also detected phylogenetic homogenization under future climates for Europe plants, birds and mammals. Clavel *et al.* (2011) reviewed the concept and consequences of functional homogenization and suggested that functional homogenization could be related to losses of biodiversity, ecosystem functioning and productivity. As the loss of rare or endemic species often

results in homogenization of the landscape (McKinney & Lockwood, 1999; Clavel *et al.*, 2011), it has become a source of concern for conservation biologists, especially considering that most species are indeed rare (*sensu* Rabenold, 1981). In particular, species that are rare due to narrow ecological amplitudes/habitat specialization have been documented from neocological and palaeocological studies as being more vulnerable to environmental change (Colles *et al.*, 2009). Our finding could be an important first step towards dealing with this concern for high-latitude regions.

Non-random extinction risk across the tree of life

Predicted responses to climate change are not randomly distributed across the plant tree of life in Alberta. Some lineages have much higher extinction risks than others, suggesting a non-random extinction risk of species' evolutionary history. This finding is supported by previous assessments using IUCN threat status (Purvis *et al.*, 2000; Vamosi & Wilson, 2008), but contrasts with two recent studies using similar approaches with predictions of species distributions and extinction risks (Thuiller *et al.*, 2011; Pio *et al.*, 2014). Random extinction risk across the tree of life was documented

for European plant species (Thuiller *et al.*, 2011) and two plant families in southern Africa (Pio *et al.*, 2014). Compared with these studies, our analyses in Alberta included nearly 90% of Alberta's total seed species, while Thuiller *et al.* (2011) included *c.* 20% of Europe plant species and Pio *et al.* (2014) focused on only two plant families in southern Africa. By using a nearly complete species list of Alberta's seed flora, our results provide strong evidence for the impacts of climate change on species' evolutionary history.

Uncertainties and perspectives

Although we have used ensemble niche models and different emission scenarios to reduce modelling uncertainty, our projections are still subject to limitations common to ENM (Franklin, 2009; Araújo & Peterson, 2012). First, species occurrence data characteristically suffer from large, unknown sampling biases due to inventory incompleteness towards regions, species and sampling efforts (Phillips *et al.*, 2009). To reduce possible effects of biased sampling on ENM, we used ensemble forecasts from five widely used ENM approaches and included recently surveyed 355 EMCLA sites in Northern Alberta, an area with low previous sampling densities (Zhang *et al.*, 2014a). In addition, Stolar & Nielsen (2015) evaluated the effects of sampling bias in ENMs for Alberta's rare vascular plants, bryophytes and butterflies, concluding that spatially biased occurrence data may not be as problematic for ENMs of rare species. For these reasons, our efforts to reduce the influence of sampling bias should result in more robust and reliable data.

Second, although the ranges of many species in Alberta extend further north and south, the wide variation in Alberta's climate provides a range of conditions making the ENMs less sensitive to geographic distribution. The climate-matching results also support this suggestion (Fig. S1). If geographic biases were strong, we would expect loss of species to be greatest in the southern grassland along the southern border of Alberta, as well as low rates of stability. The southern grasslands had some of the highest rates of stability and lowest losses of species. Regardless, the extreme ends of the environmental variation within Alberta (e.g. high elevations in the Rocky Mountains, southern grasslands and northern boreal taiga region) would be expected to have higher geographic biases in results.

Finally, species models assume environment–niche relationships and they do not acknowledge the potential for biotic interactions (Post, 2013) and other ecological feedbacks that could alter a species' niche space (Scheffer *et al.*, 2001).

CONCLUSION

Our analyses suggest that climate change will dramatically affect plant diversity and endemism patterns in Alberta. These results provide information that offers practical guidance for biodiversity conservation and management. First, our findings highlight that phylogenetic approaches may offer new oppor-

tunities for helping prioritize conservation challenges. Second, our results suggest that climate change will have a greater impact on some regions of Alberta, specifically the southern and northern parts of the Rocky Mountains, parts of the southern Grasslands and two areas of unique biogeography in the province: the Athabasca sand dunes in the north-east and the Cypress Hills in the south-west. Conservation and climate mitigation strategies should be prioritized for these regions. Third, our results offer the potential to further evaluate the effectiveness of protected areas to secure rare, endemic and evolutionarily distinct species. Fourth, our results provide baseline data for data-limited areas in northern Alberta, such as the oil sands region in north-eastern Alberta (Kurek *et al.*, 2013). Alberta's oil sands region accounts for *c.* 10% of the world's proven oil reserves (third largest petroleum reserve in the world) (OPEC, 2013). Rapid expansion of oil sands mining has raised environmental concerns about managing cumulative effects on biodiversity conservation, air and water quality, and other related environmental and social issues (Kurek *et al.*, 2013; Palen *et al.*, 2014). Plant species distributions and biodiversity maps provided here are available publicly in our 'Alberta Species Conservation Atlas' website (<http://www.ace-lab.ca/index.php?page=asca>) and are of potential value for assessments of rapid environmental changes in the region.

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REFERENCES

- ACIMS (Alberta Conservation Information Management System) (2013) Online data. Alberta Environment and Sustainable Resource Development, Edmonton, AL. Available at: [http://www.albertaparks.ca/albertaparksca/management-land-use/alberta-conservation-information-management-system-\(acims\).aspx](http://www.albertaparks.ca/albertaparksca/management-land-use/alberta-conservation-information-management-system-(acims).aspx) (accessed 12 February 2014).
- Alberta Natural Regions Committee (2006) *Natural regions and sub-regions of Alberta (compiled by D.J. Downing and W.W. Pettapiece)*. Government of Alberta, Edmonton, AL, Canada.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A.,

- Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.
- Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, **22**, 42–47.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.
- Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3**, 327–338.
- Barrow, E. & Yu, G. (2005) *Climate scenarios for Alberta*. Prairie Adaptation Research Collaborative, Regina, SA, Canada.
- Bergengren, J.C., Waliser, D.E. & Yung, Y.L. (2011) Ecological sensitivity: a biospheric view of climate change. *Climatic Change*, **107**, 433–457.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.
- Breiman, L. (2001) Random forests. *Machine learning*, **45**, 5–32.
- Chai, S.-L., Nixon, A., Zhang, J. & Nielsen, S.E. (2014) *Predicting invasive plant response to climate change: prioritization and mapping of new potential threats to Alberta's biodiversity*. Prepared for the Biodiversity Management and Climate Change Adaptation Project/Alberta Biodiversity Monitoring Institute, Edmonton, AL, Canada.
- Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Clavel, J., Julliard, R. & Devictor, V. (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, **9**, 222–228.
- Colles, A., Liow, L.H. & Prinzing, A. (2009) Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters*, **12**, 849–863.
- Crisp, M.D., Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183–198.
- Darwin, C. (1859) *On the origin of species by means of natural selection*. John Murray, London.
- Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.
- Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R. & Stocks, B.J. (2005) Future area burned in Canada. *Climatic Change*, **72**, 1–16.
- Franklin, J. (2009) *Mapping species distributions: spatial inference and predictions*. Cambridge University Press, New York, NY.
- Friedman, J.H. (2001) Greedy function approximation: a gradient boosting machine. *Annals of Statistics*, **29**, 1189–1232.
- Gould, J.A. (2007) *A habitat-based approach to rare vascular plant conservation in the northern Rocky Mountains of Alberta*. PhD Thesis, University of Alberta, Edmonton, AB, Canada.
- Hamann, A. & Wang, T.L. (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, **87**, 2773–2786.
- Hamann, A., Wang, T.L., Spittlehouse, D.L. & Murdock, T.Q. (2013) A comprehensive, high-resolution database of historical and projected climate surfaces for Western North America. *Bulletin of the American Meteorological Society*, **94**, 1307–1309.
- Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized additive models*. Chapman & Hill/CRC Press, New York.
- Hogg, E.H., Brandt, J.P. & Michaellian, M. (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research*, **38**, 1373–1384.
- IPCC (2014) *Climate change 2014: impacts, adaptation, and vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C. & Baillie, J.E.M. (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE*, **2**, e296.
- Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, 1211–1219.
- Kulig, J.J. (1996) The glaciation of the Cypress Hills of Alberta and Saskatchewan and its regional implications. *Quaternary International*, **32**, 53–77.
- Kurek, J., Kirk, J.L., Muir, D.C.G., Wang, X.W., Evans, M.S. & Smol, J.P. (2013) Legacy of a half century of Athabasca oil sands development recorded by lake ecosystems. *Proceedings of the National Academy of Sciences USA*, **110**, 1761–1766.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T. & Safranyik, L. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**, 987–990.
- Lemprière, T.C., Bernier, P.Y., Carroll, A.L., Flannigan, M.D., Gilsenan, R.P., McKenney, D.W., Hogg, E.H., Pedlar, J.H. & Blain, D. (2008) *The importance of forest sector adaptation to climate change*. Canadian Forest Service, Edmonton, AL, Canada.
- Lenoir, J. & Svenning, J.C. (2015) Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, **38**, 15–28.
- Malcolm, J.R., Markham, A., Neilson, R.P. & Garaci, M. (2002) Estimated migration rates under scenarios of global climate change. *Journal of Biogeography*, **29**, 835–849.

- Marquardt, D.W. (1970) Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics*, **12**, 591–612.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, **14**, 450–453.
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: biodiversity synthesis*. Island Press, Washington, DC.
- Minteer, B.A. & Collins, J.P. (2010) Move it or lose it? The ecological ethics of relocating species under climate change. *Ecological Applications*, **20**, 1801–1804.
- Moss, E.H. (1983) *Flora of Alberta: a manual, ferns of flowering plants, conifers and fern allies found growing without cultivation in the province of Alberta*. University of Toronto Press, Toronto, ON, Canada.
- Nakicenovic, N. (2000) *Special report on emissions scenarios: a special report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- NatureServe (2014) NatureServe explorer: an online encyclopedia of life [web application]. Version 7.0. Available at: <http://explorer.natureserve.org/> (accessed 6 June 2014).
- Nielsen, S.E., Boyce, M.S., Stenhouse, G.B. & Munro, R.H.M. (2003) Development and testing of phenologically driven grizzly bear habitat models. *Ecoscience*, **10**, 1–10.
- Nielsen, S.E., McDermid, G., Stenhouse, G.B. & Boyce, M.S. (2010) Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biological Conservation*, **143**, 1623–1634.
- OPEC (2013) OPEC (Organization of the Petroleum Exporting Countries) *Annual Statistical Bulletin 2013*. Available at: www.opec.org/opec_web/en/publications/202.htm (accessed 8 October 2014).
- Palen, W.J., Sisk, T.D., Ryan, M.E., Arvai, J.L., Jaccard, M., Salomon, A.K., Homer-Dixon, T. & Lertzman, K.P. (2014) Consider the global impacts of oil pipelines. *Nature*, **510**, 465–467.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological niches and geographic distributions*. Princeton University Press, Princeton, NJ.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**, 1246752.
- Pio, D.V., Engler, R., Linder, H.P., Monadjem, A., Cotterill, F.P.D., Taylor, P.J., Schoeman, M.C., Price, B.W., Villet, M.H., Eick, G., Salamin, N. & Guisan, A. (2014) Climate change effects on animal and plant phylogenetic diversity in southern Africa. *Global Change Biology*, **20**, 1538–1549.
- Post, E. (2013) *Ecology of climate change: the importance of biotic interactions*. Princeton University Press, Princeton, NJ.
- Price, D.T., McKenney, D.W., Joyce, L.A., Siltanen, R.M., Papadopol, P. & Lawrence, K. (2011) *High resolution interpolation of IPCC AR4 GCM climate scenarios for Canada*. Natural Resources Canada, Canadian Forest Service, Edmonton, AL, Canada.
- Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., McKenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J.A. & Venier, L.A. (2013) Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews*, **21**, 322–365.
- Purvis, A., Agapow, P.M., Gittleman, J.L. & Mace, G.M. (2000) Nonrandom extinction and the loss of evolutionary history. *Science*, **288**, 328–330.
- R Core Team (2014) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rabinowitz, D. (1981) Seven forms of rarity. *The biological aspects of rare plants conservation* (ed. by H. Synge), pp. 205–217. Wiley, New York, NY.
- Raup, H.M. & Argus, G.W. (1982) *The Lake Athabasca sand dunes of Northern Saskatchewan and Alberta, Canada*. National Museums of Canada, Ottawa, ON, Canada.
- Roquet, C., Thuiller, W. & Lavergne, S. (2013) Building megaphylogenies for macroecology: taking up the challenge. *Ecography*, **36**, 13–26.
- Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C. & Cook, L.G. (2009) Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, **18**, 4061–4072.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.
- Stolar, J. & Nielsen, S.E. (2015) Accounting for spatially-biased sampling effort in presence-only species distribution modelling. *Diversity and Distributions*, **5**, 595–608.
- Stralberg, D., Matsuoka, S.M., Hamann, A., Bayne, E.M., Sólymos, P., Schmiegelow, F., Wang, X., Cumming, S.G. & Song, S.J. (2015) Projecting boreal bird responses to climate change: the signal exceeds the noise. *Ecological Applications*, **25**, 52–69.
- Thomas, C.D. (2011) Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology and Evolution*, **26**, 216–221.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de

- Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller, W. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.
- Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.
- Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B. & Araújo, M.B. (2011) Consequences of climate change on the tree of life in Europe. *Nature*, **470**, 531–534.
- Thuiller, W., Guéguen, M., Georges, D., Bonet, R., Chalmandrier, L., Garraud, L., Renaud, J., Roquet, C., Van Es, J., Zimmermann, N.E. & Lavergne, S. (2014) Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. *Ecography*, **12**, 1254–1266.
- Vamosi, J.C. & Wilson, J.R.U. (2008) Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecology Letters*, **11**, 1047–1053.
- Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist*, **156**, 145–155.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.
- Winter, M., Devictor, V. & Schweiger, O. (2013) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology and Evolution*, **28**, 199–204.
- Yesson, C., Brewer, P.W., Sutton, T., Caithness, N., Pahwa, J.S., Burgess, M., Gray, W.A., White, R.J., Jones, A.C., Bisby, F.A. & Culham, A. (2007) How global is the global biodiversity information facility? *PLoS ONE*, **2**, e1124.
- Zanne, A.E., Tank, D.C., Cornwell, W.K. et al. (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature*, **506**, 89–92.
- Zhang, J., Nielsen, S.E., Grainger, T.N., Kohler, M., Chipchar, T. & Farr, D.R. (2014a) Sampling plant diversity and rarity at landscape scales: importance of sampling time in species detectability. *PLoS ONE*, **9**, e103920.
- Zhang, J., Huang, S., Hogg, E.H., Lieffers, V., Qin, Y. & He, F. (2014b) Estimating spatial variation in Alberta forest biomass from a combination of forest inventory and remote sensing data. *Biogeosciences*, **11**, 2793–2808.
- Zhang, J., Mayor, S.J. & He, F. (2014c) Does disturbance regime change community assembly of angiosperm plant communities in the boreal forest? *Journal of Plant Ecology*, **7**, 188–201.
- Zhang, J., Huang, S. & He, F. (2015) Half-century evidence from western Canada shows forest dynamics is primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences USA*, **112**, 4009–4014.

SUPPORTING INFORMATION

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

Appendix S1 Additional methods.

Table S1 Species list of 1541 seed plants occurred in Alberta, Canada.

Figure S1 Climatic matching between Alberta and other regions in North America north of Mexico.

Figure S2 Comparison of ENM results under current climate for data from Alberta-only and from Alberta and its two-degree neighbour regions.

Figure S3 Species' vulnerability to climate change by 2080s with respect to their growth forms.

Figure S4 Species' vulnerability to climate change by 2080s with respect to their NatureServe subnational rarity status.

Figure S5 Maps of species richness and phylogenetic diversity under the current and future periods.

Figure S6 Refugia, gains and losses of Alberta seed plants projected under the A1B emissions scenario (GCM: CGCM3) in 2080s.

Figure S7 Maps of taxonomic endemism and phylogenetic endemism under the current and future periods.

Figure S8 Spatial and temporal variations of phylogenetic relatedness under current and projected distributions in 2080s under the A1B emissions scenario (GCM: CGCM3).

BIOSKETCH

Jian Zhang is currently a researcher at Aarhus University, Denmark. His research interests include macroecology, conservation biogeography, community ecology and forest dynamics.

Author contributions: J.Z., S.E.N. and W.T. conceived the ideas and designed the study; J.Z., S.E.N., J.S. and Y.C. collected and analysed data; and all authors contributed to the content of the manuscript.

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