Diversity and Distributions, (Diversity Distrib.) (2009) **15**, 972–982

A Journal of Conservation Biogeography
Diversity and Distributions

BIODIVERSITY RESEARCH

The coastal-disjunct mesic flora in the inland Pacific Northwest of USA and Canada: refugia, dispersal and disequilibrium

Daniel G. Gavin*

Department of Geography, University of Oregon, Eugene, OR 97403-1251, USA

ABSTRACT

Aim Understanding the history of the mesic-adapted plant species of eastern British Columbia and northern Idaho, disjunct from their main coastal distribution, may suggest how biotas reorganize in the face of climate change and dispersal barriers. For different species, current evidence supports establishment of the disjunction via an inland glacial refugium, via recent dispersal from the coast, or via a combination of both. In this study, the modern distributions of the coastal-disjunct vascular plants are analysed with respect to modern climate to examine how refugia and/or dispersal limitation control regional patterns in species richness.

Location North-west North America.

Methods The distributions of nine tree and 58 understorey species with a coastal-disjunct pattern were compiled on a 50-km grid. The relationship between species richness and an estimate of available moisture was calculated separately for formerly glaciated and unglaciated portions of the coastal and inland regions. Growth habit and dispersal mode were assessed as possible explanatory variables for species distributions.

Results Species richness shows a strong relationship to climate in coastal-unglaciated areas but no relationship to climate in inland-glaciated areas. In inland-glaciated areas, richness is *c.* 70% lower than that expected from climate. Species with animal-dispersed seeds occupy a larger portion of coastal and inland regions than species with less dispersal potential.

Main conclusions Modern patterns of diversity are consistent with both refugia and dispersal processes in establishing the coastal-disjunct pattern. The inland glacial refugium is marked by locally high diversity and several co-distributed endemics. In the inland-glaciated area, dispersal limitation has constrained diversity despite the nearby refugia. Onset of mesic climate within only the last 3000 years and the low dispersal capacity of many species in the refugium may explain this pattern. This study suggests that vascular plant species will face significant challenges responding to climate change on fragmented landscapes.

*Correspondence: Daniel G. Gavin, Department of Geography, 1251 University of Oregon, Eugene, OR 97403-1251, USA.
E-mail: dgavin@uoregon.edu

Keywords

Cordilleran ice sheet, dispersal barrier, glacial refugium, Idaho, *Thuja plicata*, *Tsuga heterophylla*.

INTRODUCTION

Retrospective studies of how biotas reorganize through climate fluctuations may reveal many aspects of species that are difficult to measure directly, but understanding of which is greatly needed to constrain predictions of climate change impacts on biodiversity (Botkin *et al.*, 2007). For example, species persistence in small populations (refugia) embedded within a regionally unfavourable climate may indicate a capacity for acclimatization and a broader fundamental niche

DOI: 10.1111/j.1472-4642.2009.00597.x
www.blackwellpublishing.com/ddi

than otherwise observed on the modern landscape (Williams & Jackson, 2007). Similarly, evidence of dispersal over large barriers, or the lack of successful dispersal and establishment, may indicate the dispersal potential of species for which long-distance dispersal capacity is unknown (Higgins & Harte, 2006). A particularly useful setting for studying these processes is a climatically heterogeneous region that supports several species with broadly similar climatic requirements and which are co-distributed in one or more disjunctions. The alternate histories underlying disjunctions are (1) expansion from predispersed populations (i.e. refugia possibly dating back to an earlier vicariance event), (2) colonization by long-distance dispersal, or (3) a mixture of both processes (McDowall, 2004).

A set of species with such a disjunct pattern is the mesic-adapted biota of north-west North America, where at least 156 species or species complexes have a main coastal distribution and a disjunct inland distribution in the Columbia Mountains of British Columbia and northern Rocky Mountains of Idaho and Montana (Nielson *et al.*, 2001; Fig. 1). A dry rainshadow climate in eastern Oregon, Washington, and British Columbia causes a barrier of > 160 km separating the coastal and inland regions, though three marginally mesic mountainous areas span the barrier and support small outlier populations of a few mesic-adapted species (Frenkel, 1974; Daubenmire, 1975). Most of the inland mesic habitat occurs in formerly glaciated terrain that was rapidly deglaciated from *c.* 16,500 to 13,000 years before present (BP; Dyke *et al.*, 2003). These areas may have been colonized from populations surviving in several deeply incised river canyons of unglaciated northern Idaho (the 'Clearwater Refugium'), and/or by dispersal from the coast via one or more highland routes (Fig. 1).

Various lines of evidence support either dispersal or refugia explanations for individual taxa. Based on modern species distributions, Daubenmire (1952) hypothesized that an ancient vicariance event was responsible for the disjunct mesic flora, being '…the hardier elements of the montane Miocene forest which have been able to persist to the leeward of the Cascade climatic barrier, despite the great changes which came about when these mountains were uplifted'. The existence of a mesic Clearwater Refugium has been supported by several phylogeographic studies that show (1) ancient divergence of coastal-inland amphibian sister-species and (2) compartmentalized refugia of north-Idaho endemic species (Table 1). However, other phylogeographic studies of single species with the disjunct pattern have supported a recent dispersal from the coast. For example, *Thuja plicata*, a tree species that encompasses the entire inland mesic region and with which most coastal-disjuncts are closely affiliated, was shown to have recently dispersed from the coast (O'Connell *et al.*, 2008). Pollen records and other climate reconstructions indicate that *Thuja plicata* and the other dominant mesic tree species, *Tsuga heterophylla*, were absent or rare before *c.* 3500 yr BP (Mehringer, 1996). North of the Clearwater Refugium in western Montana, *Tsuga heterophylla* was consistently present only after 2400 yr BP (Chatters & Leavell, 1994). Mesic habitat was likely spatially patchy prior to 3500 yr BP, providing a challenging landscape for long-distance dispersal. Several other studies supporting refugia, dispersal, or a complex history of refugia followed by limited dispersal, are listed in Table 1.

In this study, I present the modern patterns of diversity of the coastal-disjunct vascular plant species in north-west North America. Although modern distributions provide only indirect evidence of historical processes, correlation of species distributions with glacial history, climate, and species traits may reveal a discernible fingerprint of refugia or limited dispersal (Currie, 2007). Lorain (1988) produced distribution maps of 53 coastal-disjunct vascular plant species using extensive literature searches, herbarium visits and field verification.

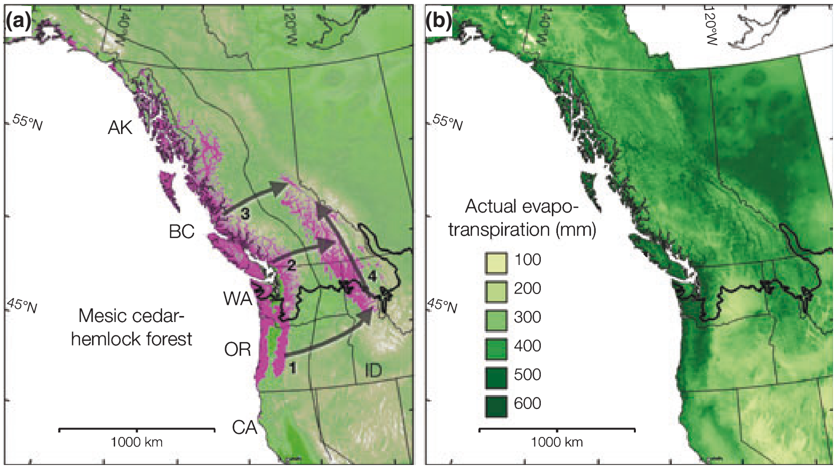

Figure 1 (a) The distribution of *Tsuga–Thuja* forest in north-west North America (magenta) plotted on a topographic map. Arrows 1–4 show possible dispersal routes for colonizing the inland region. 1: Ochoco Connection, 2: Okanagan Highlands, 3: Chilcotin Connection, 4: 'out of the Clearwater Refugium'. The thick black line shows the extent of the Cordilleran ice sheet and proglacial lakes at 18,000 yr BP. The thin black line shows the division between 'coastal' and 'inland' used in this study. (b) Annual actual evapotranspiration estimated from monthly temperature and precipitation. All map projections are Albers Equal-Area.

Table 1 Evidence supporting various biogeographical histories of the mesic disjunct biota of the inland north-west North America. Both plant an animal studies are shown.

Method	Evidence for Clearwater Refugium	Evidence for dispersal from coast (and likely route from Fig. 1)
Palaeorecords*	No palaeorecords exist within the refugium. Most proximal to refugium indicate cold/dry late Pleistocene (see text)	*Tsuga heterophylla* and *Thuja plicata* (**2,3**) (Mehringer, 1996)
Phylogeography†	Time since divergence (coastal/inland sister taxa) *Dicamptodon tenebrosus*/*Dicamptodon aterrimus* (Steele *et al.*, 2005) *Plethodon vandykei*/*Plethodon idahoensis* (Carstens *et al.*, 2004) *Ascaphus truei*/*Ascaphus montanus* (Nielson *et al.*, 2001) *Pinus albicaulis* (Richardson *et al.*, 2002) Compartmentalized Clearwater refugium *Ascaphus montanus* (Nielson *et al.*, 2001) *Cardamine constancei* (Brunsfeld & Sullivan, 2005) *Salix melanopsis* (Brunsfeld *et al.*, 2007) *Tamias ruficaudus* (Good & Sullivan, 2001)	*Alnus rubra* (**1**) (Strenge, 1994) *Microtus richardsoni* (**2**) (Carstens *et al.*, 2005) *Pinus albicaulis* (**2**) (Richardson *et al.*, 2002) *Polystichum munitum* (**1**) (Strenge, 1994) *Salix melanopsis* (**2**) (Brunsfeld *et al.*, 2007) *Tellima grandiflora* (**2**) (Soltis *et al.*, 1991) *Tiarella trifoliata* (**2**) (Soltis *et al.*, 1992) *Thuja plicata* (**1,2**) (O'Connell *et al.*, 2008)
Modern species distributions‡	All six north-Idaho endemic vascular plant species are restricted south of the glacial maximum; several coastal disjuncts have inland distributions entirely south of glacial maximum (Lorain, 1988) *Tsuga mertensiana* is concentrated immediately south of the glacial maximum, and is patchy north of this limit (Cooper *et al.*, 1991)	Lichen diversity centred in British Columbia, far north of refugia (Goward & Spribille, 2005) *Tsuga heterophylla* southern limit not climatically determined (Gavin & Hu, 2006)

*In general, pollen records rarely detect the presence of small refugial populations, but they do reveal the spatiotemporal dynamics of the dominant vegetation. Rosenberg *et al.* (2003) did not support any dispersal scenario for *Tsuga heterophylla.*

†Phylogeographic studies included here are limited to those based on cpDNA, mtDNA, or microsatellites, and are reviewed in Soltis *et al.* (1997), Brunsfeld *et al.* (2001) and Carstens *et al.* (2005). Two additional studies of tree species were inconclusive but suggestive of dispersal from the coast: *Tsuga heterophylla,* based on RFLPs and cpDNA (Peery, 2005) and *Cornus nuttallii*, based on isozymes and RAPDs [S.J. Brunsfeld & L.M. Rieseberg, 1993, *American Journal of Botany*, **80** (6), p. 134]. Note that both *Pinus albicaulis* and *Salix melanopsis* support both refugia followed by limited dispersal (including inland-to-coast dispersal). *Pinus albicaulis* and *Tiarella trifoliata* do not meet the definition of a coastal-disjunct used in this study (see Methods).

‡Analysis of modern species distributions of vascular plants is the focus of this study and is therefore abbreviated in this table.

From this study, nearly half (26 species) have inland distributions that broadly suggest a glacial refugium. This study expands upon Lorain (1988) by comparing richness–climate relationships among regions and using species traits as a possible explanatory factor for evidence of disequilibrium of modern species ranges with climate. Based on previous work that detected a general effect of glacial history on patterns of tree richness (Montoya *et al.*, 2007), I expect to detect some degree of disequilibrium between species distribution and their potential range, explainable by limited dispersal into glaciated areas. Greater disequilibrium could result from a large dispersal barrier; less disequilibrium could result from dispersal out of a species-rich inland refugium.

I address these specific questions: (1) How does species richness of coastal-disjunct plants vary with climate, and is this relationship markedly different between coastal and inland regions and between glaciated and unglaciated regions? If recolonization of formerly glaciated areas and the inland regions is not limited by dispersal, then richness–climate relationships should differ minimally among areas. (2) Which dispersal and refugia scenarios are supported by modern patterns of species assemblages? If the majority of the inland disjunctions originated from an 'out of the Clearwater Refugium' scenario, then inland species richness should decline monotonically with latitude and great dissimilarity should exist between coastal and inland species assemblages. (3) Does growth habit and seed-dispersal mode explain the spatial extent of species distributions? If dispersal limitation were not an important factor affecting species richness in isolated areas (i.e. inland-glaciated areas), then species traits related to dispersal potential and fecundity should not be biased with respect to glacial history.

METHODS

Species selected were those with a marked coastal-disjunct pattern (i.e. lacking a continuous distribution to the Rocky Mountains), not extending eastward into boreal forest or southward into the southern Rocky Mountains. Aquatic plants and species mainly occurring in alpine meadows were also excluded. Coastal-disjunct and north-Idaho endemic species were identified from published accounts (Little, 1971; Johnson & Steele, 1978; Lorain, 1988; Douglas, 1996). The final species list included nine tree and 58 understorey coastal-disjunct species and six north-Idaho endemic species (see Appendix S1 in Supporting Information, for species lists).

Species distributions were compiled from occurrences of vouchered specimens and observations using a several-step process. First, the maps in Lorain (1988) were scanned and rectified to an Albers projection in GRASS GIS. These maps were digitized as polygons where data suggested a continuous (< 50-km resolution) distribution, or as points where continuous distributions were not known. Unverified outlier occurrences reported in Lorain (1988) were not included. Second, occurrences of herbarium specimens reported in the Global Biodiversity Information Facility (http://www.gbif.org) were added as point locations, excluding points with a > 20 km location uncertainty (e.g. county-level occurrences). As few Canadian sources are reported in GBIF, occurrences in British Columbia were obtained from several datasets presented in E-flora BC (http://www.eflora.bc.ca). These occurrences were digitized from map images because the raw data were unavailable except for the University of British Columbia herbarium records. Since numerous georeferencing errors were detected in E-flora BC, single spatial outliers (> 50 km from other occurrences) were included only if the record had additional location information and was a herbarium specimen. The nine tree species were mapped from Little (1971) and augmented by herbarium records as above. For each species, all data sources were overlayed and distributions generalized to a 50-km grid.

Groups of similar species assemblages were determined using a *k*-means cluster analysis based on the Bray–Curtis distance (Proches, 2005). For both the tree and understorey species groups, five clusters explained an optimal amount of variance as determined by an inflection in a plot of residual variance vs. number of clusters.

Previous work has shown that a single bioclimatic variable, an estimate of the annual actual evapotranspiration (AET), is a very effective predictor of the range of the mesic-adapted canopy dominant *Tsuga heterophylla* (Gavin & Hu, 2006). AET, an integrator of the water and energy available for primary productivity, is widely used as predictor of woody plant richness in general (Currie, 1991; Field *et al.*, 2009) and in the study area (Daubenmire, 1956; Jennings *et al.*, 2005). To account for the large amount of climatic variability within each 50-km grid cell in which species presence is summarized, AET was calculated for the most mesic 10% of each 50-km grid cell using the following steps. First, climate data (1970–99 monthly normals) from a 2.5-min resolution dataset (PRISM; Daly *et al.*, 1994) were downscaled onto a 15-arc-second (*c.* 400 m) elevation grid using locally derived lapse rates (CLIMATEBC software; Wang *et al.*, 2006). Second, AET was estimated using a modified Thornthwaite climatological water balance (Willmott *et al.*, 1985). To include topographic effects on the energy balance, potential evapotranspiration was scaled to account for slope, aspect and hillshading using the r.sun command in GRASS GIS. Third, AET was projected to an Albers Equal-Area projection at 400-m resolution. Last, the 90th percentile of AET values in each 50-km grid cell was retained for further analysis (AET_{90}; i.e. 10% or 250 km^2 in each 50-km grid cell has an AET greater than AET_{90}).

Regression models were fitted to species richness as a function of AET_{90}. It is expected that species richness of the subset of mesic-adapted species selected for this analysis would have a step-like relationship with AET_{90}, and therefore a four-parameter logistic regression was used. Four models were fitted to tree and understorey species by dividing the data set into glaciated and unglaciated portions of the coastal and inland regions.

Last, the spatial extent of understorey distributions was summarized relative to species traits. Traits were summarized as growth habit (graminoid, forb, dwarf shrub, or shrub) and dispersal mode (animal, wind, explosive-ballistic, ant, or an 'other' group for non-adapted, unknown, or short-distance dispersal modes such as splash cups and censer mechanisms). Species range sizes calculated from the 50-km resolution maps were compared among trait groups using the Mann–Whitney *U*-test. To determine whether dispersal-related traits are biased with respect to occurrence within and outside of the Clearwater Refugium, species were classified according to their inland distribution pattern (restriction to glaciated, unglaciated, or both areas) and their traits (growth habit and dispersal mode). Interactions in the distribution × growth habit and distribution × dispersal mode matrices were tested using chi-square statistics.

RESULTS

Richness of coastal-disjunct tree species is greatest in the coastal region from south-west British Columbia to western Oregon, while inland richness was greatest in northern Idaho and declines steadily northward (Fig. 2). Understorey species richness follows a similar pattern with the exception that the inland region supports two centres of high richness, one south and one north of the glacial-maximum limit. Cluster analysis shows a latitudinal zonation of tree species assemblages along the coast while inland assemblages are unlike any on the coast except in the northern and southern ends of the inland region. Understorey species assemblages also cluster latitudinally, though most of the inland grid cells cluster with the eastern-most portion of the coastal region, while the core, high-diversity, inland areas cluster with the western-most portion of the coastal region.

Tree species richness in unglaciated areas shows a step response with AET_{90} ($r^2 = 0.74$ and 0.76 in coastal and inland areas respectively), as would be expected for the mesic-adapted species included in this analysis (Fig. 3). Understorey species richness shows a similar step response in unglaciated areas, though much weaker in the inland portion ($r^2 = 0.91$ and 0.28 in coastal and inland areas respectively). In contrast, these relationships are much weaker in coastal-glaciated areas

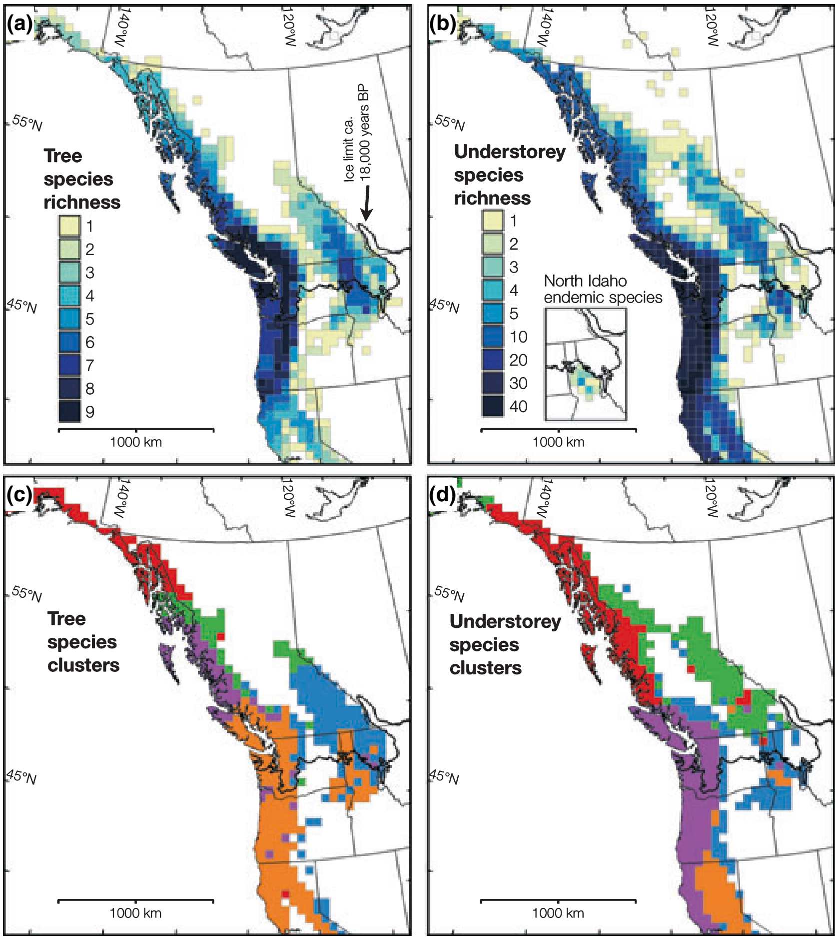

Figure 2 Patterns of species richness of (a) nine tree and (b) 58 understorey vascular plant species that display a coastal-disjunct distribution pattern (i.e. species with a main coastal distribution and disjunct occurrences in the northern Rocky Mountains). Extent of the Cordilleran ice sheet is shown as in Fig. 1. Inset map shows species richness of six northern Idaho endemic plant species. Data are summarized as presence in 50-km grid cells. Note the colour gradient chosen to emphasize variability at lower richness levels. (c,d) Clustering of species assemblages for tree and understorey species in cells containing ≥ 2 species. See Appendix S1 for species lists.

(r^2 = 0.27 and 0.34 for tree and understorey species respectively) and no relationship occurs for inland-glaciated areas. These low correlations are the result of lowered richness in glaciated areas compared to that expected from the AET_{90}–richness relationship in unglaciated areas. Specifically, richness in many grid cells was often 30% (for understorey species) to 50% (for tree species) of that expected from the unglaciated-area relationships.

There is no pattern among growth habits with respect to glacial history in the inland region ($\chi^2 = 9.7$, $P = 0.138$; Table 2). In contrast, dispersal modes are not randomly partitioned among glaciated and unglaciated areas ($\chi^2 = 15.0$, $P = 0.020$; Table 2). A greater number of species with animal-dispersal modes have inland distributions restricted to glaciated areas and a greater number of species with ‘other’ (non-adapted or limited) dispersal modes are restricted to inland-unglaciated areas than expected by chance.

Overall, understorey species occupy a greater percentage of the coastal region than the inland region (Fig. 4). Furthermore, in both coastal and inland regions, species with animal dispersed seeds occupy a greater area than species with other dispersal modes, though there is much variability among species within each dispersal mode. In contrast, there is no significant difference among growth habits in percentage area occupied in either coastal or inland regions.

DISCUSSION

The spatial patterns of coastal-disjunct plant species have been strongly influenced by dispersal limitation and the presence of an inland mesic refugium. In coastal-unglaciated areas where most mesic-adapted species probably occurred during the last glaciation (Whitlock, 1992), the relationship between species richness and climate shows a distinct step response, indicating that mesic-adapted species have extended their ranges into all areas that are sufficiently moist. This relationship deteriorates dramatically in inland and glaciated areas. Many species have extended their range only a short distance into glaciated areas, such that areas north of *c.* 200 km from the glacial maximum support only *c.* 30% of the understorey species that are expected from the climate–richness relationship in unglaciated areas (Fig. 2). In inland areas, where many species had to first disperse over a large rainshadow barrier and where widespread mesic conditions have existed for < 3500 years, there is no climate–richness relationship. For tree species, although the level of disequilibrium is less severe (*c.* 50% underdispersed), it remains close to the upper end of values found at the continental scale (Montoya *et al.*, 2007) and the degree of disequilibrium suggested by Latham & Ricklefs (1993) and McGlone (1996). In addition, these patterns contrast strongly with a similar study by Goward & Spribille (2005) that found

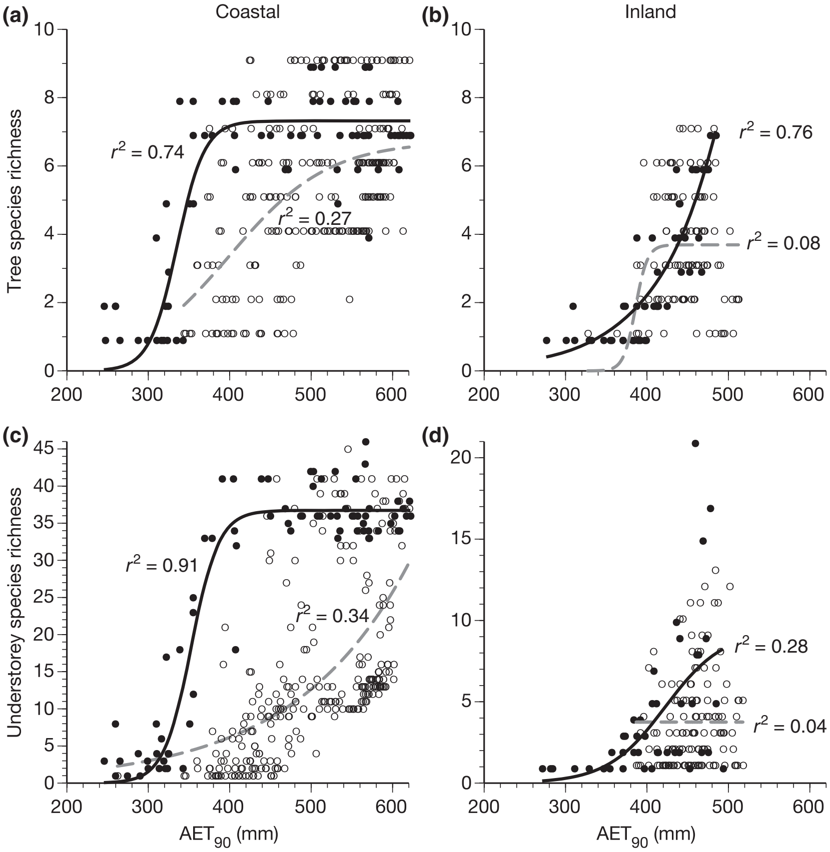

Figure 3 Relationship between species richness and climate in 50-km grid cells for tree (a,b) and understorey (c,d) species. Glaciated areas (open symbols and dashed curve fit) and unglaciated areas (closed symbols and solid curve fit) are plotted together. Curve fits are a four-parameter logistic model. Symbols from glaciated and unglaciated areas are offset vertically for clarity. Climate (AET_{90}) is the 90th percentile of the distribution of actual evapotranspiration estimates within each 50-km grid cell.

Table 2 Numbers of understorey species grouped by their distribution in the inland region and by two traits: growth habitat or predominant dispersal mode. Values in parentheses indicate the expected number of species if there were no trait × distribution interaction. Three types of inland distributions are summarized: both glaciated and unglaciated areas, restricted to glaciated areas and restricted to unglaciated areas. Growth habit did not interact with distribution patterns ($\chi^2 = 9.7$, $P = 0.138$), but dispersal mode showed a strong interaction with distribution pattern ($\chi^2 = 15.0$, $P = 0.020$).

	Number of understorey species			
	Glaciated and unglaciated	Glaciated only	Unglaciated only	Total
Growth habit				
Graminoid	1 (2.17)	1 (2.05)	5 (2.78)	7
Forb	9 (11.17)	12 (10.55)	15 (14.28)	36
Dwarf shrub	3 (1.24)	0 (1.17)	1 (1.59)	4
Shrub	5 (3.41)	4 (3.22)	2 (4.36)	11
Dispersal mode				
Animal	6 (4.66)	7 (4.40)	2 (5.95)	15
Wind	7 (5.59)	6 (5.28)	5 (7.14)	18
Ballistic and ant	2 (1.86)	2 (1.76)	2 (2.38)	6
Other	3 (5.90)	2 (5.57)	14 (7.53)	19
Total	18	17	23	58

the highest diversity of epiphytic macrolichens in the wettest portions of the inland-glaciated areas, thus suggesting little dispersal limitation. This contrast is not surprising considering the high dispersal potential of spores compared to most vascular plant seeds. Additional climate variables, if added to the analysis, may reduce the degree of disequilibrium suggested here, but doing so also would increase the risk of assigning climatic envelopes that are too narrow if the species are indeed not occupying their potential range (Svenning & Skov, 2004).

Various lines of evidence support the importance of low dispersal and establishment limiting the richness of the coastal-disjunct plants. First, species with the greatest dispersal potential (i.e. animal-dispersed berries) have the largest geographical ranges (Fig. 4) and are more likely than other groups to have reached the inland-glaciated region (Table 2). Occasional dispersal by non-standard modes such as accidental ingestion by an ungulate (Cain *et al*., 1998) may explain why some species with low dispersal potential occur far north of the glacial limit (e.g. *Tellima grandiflora* with a censer mechanism). This study suggests that such non-standard dispersal may be the exception rather than the rule. Second, in the inland-unglaciated area, there is a stronger climate–richness relationship for trees than for understorey species (Fig. 2). The high fecundity of tree species compared to herb and shrub species should result in tree species reaching relatively more of the available habitat, though longer generation times of tree vs. understorey species may counter any advantage of widespread dispersal. In inland-glaciated areas, several tree species have not reached their potential distribution, as suggested by the patchy distribution of *Tsuga mertensiana* and the fact that *Xanthocyparis nootkatensis* is being successfully planted

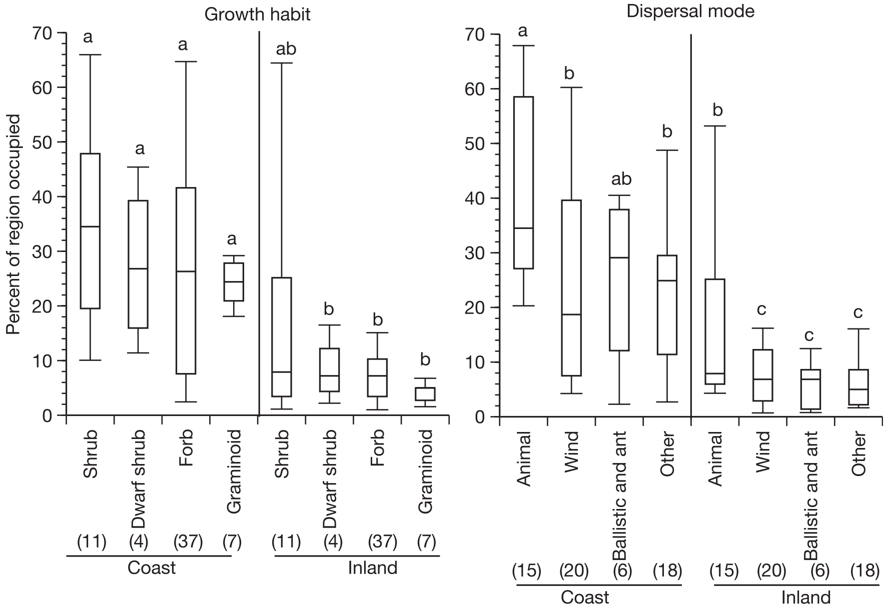

Figure 4 The percentage of the coastal or inland regions occupied (defined by the 50-km grid cells with at least two coastal-disjunct species present) for species grouped by growth habit or dispersal mode. Box plots show the 10th, 25th, 50th, 75th and 90th percentiles for each set of species. Different letters above box plots group indicate a significant difference as determined by a Mann–Whitney *U*-test. Sample sizes (number of species) are in parentheses.

following logging in areas 135 km north of its only naturally occurring inland population in south-eastern British Columbia. Overall, these patterns suggest that additional investigation into long-distance dispersal potential (e.g. palatability and gut survival) may further explain the spatial extent of coastal-disjunct species.

The clustering of species assemblages reveals general patterns of species co-occurrence and thus may reveal patterns consistent with certain dispersal routes and climatic controls. If inland-glaciated areas were colonized from the coast and unglaciated areas were colonized from proximal refugia, then the inland-glaciated and unglaciated areas should support distinct clusters. However, if inland-glaciated areas were colonized from the refugium, then the entire inland region should support a single cluster. Neither appears to be the case. Tree assemblages show a mirroring of clusters between the coast and inland regions in the north and south, but not in the centre, suggesting that the inland region represents a broad mixture of species entering from either end (Fig. 1). In contrast, understorey species clusters are similar to the clusters in the eastern portion of the coastal regions at the same latitude. This pattern may reflect the climatic similarity of the inland region with the inland portion of the coastal region in central British Columbia, or it may reflect a dispersal route from the north. An exception is that some of the core inland areas with high species richness correspond with assemblages from the coast, indicating the oceanic affinities of the wettest portions of the inland region. Thus, while the clustering patterns are consistent with the effects of both climate and dispersal on inland species composition, it does not show species assemblages from the Clearwater Refugium extending northward. Furthermore, an ‘out of the Clearwater’ hypothesis should result in a monotonically decreasing richness northward from Idaho, which is clearly not the case for the understorey species (Fig. 2). Indeed, 17 of 58 understorey species have inland distributions restricted to glaciated areas (Table 2). Thus, colonization of inland-glaciated areas via dispersal from the coast was likely at least as important as expansion from the Clearwater Refugium.

The palaeoecological record, though sparse in the inland region, is consistent with a coastal origin for species in the inland-glaciated area. The earliest increase in *Tsuga heterophylla* pollen in the inland region (4500 yr BP) occurs between the Okanagan and Chilcotin routes (Gavin, unpublished data), suggesting a north-to-south establishment of the mesic forest type. Several pollen records south-west of this site in the Okanagan Highlands found no evidence of a mesic climate similar to today prior to *c.* 3000 yr BP (Pellatt *et al.*, 1998; Heinrichs *et al.*, 2002). Thus, if *Tsuga heterophylla* pollen records are interpreted as indicating regional arrival times and dispersal routes, this tree species would have had to disperse over a > 100-km wide xeric barrier. However, pollen data cannot reliably detect absolute distribution limits (McLachlan & Clark, 2004). Furthermore, several phylogeographic studies propose that the Okanagan Highlands was a post-glacial dispersal corridor (Table 1), and thus sufficient microsites in this region may have aided *Tsuga heterophylla* eastward range extension. The northern (Chilcotin) route for *Tsuga heterophylla* during the early Holocene was hypothesized by Hansen (1955), but *Tsuga heterophylla* pollen first increases in the northern-inland region only *c.* 2000 yr BP (Gavin *et al.*, 2009). Similarly, the southern (Ochoco) route has been proposed for several other tree species on the basis of phylogeography (Table 1).

Despite the considerable evidence for dispersal from the coast, species distributions also support the existence of the Clearwater Refugium. Overall, 40% of the understorey species have inland distributions that are consistent with their origin from the Clearwater Refugium (23 of 58 species have inland distributions restricted to unglaciated areas; Table 2). In several grid cells immediately south of the inland-glaciated region, locally high species richness of coastal-disjuncts is greater than that expected from the general inland richness–climate relationship, but still lower than that expected based on the relationship from the coastal region (Fig. 3). Furthermore, these areas of high richness co-occur with six north-Idaho endemic plant species. While several phylogeographic studies support the existence of compartmentalized mesic glacial refugia in several canyons of the Clearwater River system (Table 1; Brunsfeld *et al.*, 2007), no pollen records exist within or near the refugium and little palaeoclimate information exists from the region to aid in characterizing the refugium.

The climate that existed south of the Cordilleran ice sheet during the last glacial maximum was significantly colder, and potentially drier, than today. Vegetation inferred from fossil phytoliths preserved in loess sequences of south-eastern Washington indicates reduced forest cover and cold/dry conditions for most of the Pleistocene (Blinnikov *et al.*, 2002). Climate simulations for the last glacial maximum (21,000 yr BP) in the refugium area show a temperature decrease of *c.* 10 °C (though ameliorating quickly southward) and slightly decreased precipitation (Otto-Bliesner *et al.*, 2006). Following the glacial maximum, the northward shift of the jet stream, the weakening of the easterly glacial anticyclone, and the intensification of Northern Hemisphere seasonality resulted in increased westerly moisture flow (Bartlein *et al.*, 1998). Pollen records and alpine glacial advances indicate increasing moisture before 14,000 yr BP (Brunelle & Whitlock, 2003; Thackray *et al.*, 2004). During the transition to Holocene climate, midge records from southern British Columbia reveal an increase in summer temperature from −3 to +5 °C relative to modern (Chase *et al.*, 2008). In general, from *c.* 11,000 to *c.* 6000 yr BP, the region experienced warm and dry summer conditions with modern mesic conditions establishing within the last 3000 years (Thompson *et al.*, 1993). These results suggest that mesic refugia during the Pleistocene would have likely been displaced significantly downslope (westward) out of the region of high orographic precipitation, and then during the early Holocene displaced upslope above its current location.

The above discussion presents a conflict between the climate inferred from the Pleistocene palaeorecords and the existence of mesic refugia inferred from genetic and biogeographical data. Similarly, anomalous cryptic northern refugia have been identified in Europe (Stewart & Lister, 2001) and eastern North America (McLachlan *et al.*, 2005). One resolution to this paradox may be that climate was indeed not as dry as suggested from the pollen data due to the impact of low atmospheric CO_2 concentration on tree cover (Cowling & Sykes, 1999). While the marginal effect of CO_2 on vegetation-climate relationships may be debated, a second resolution to the paradox may simply lie in the great environmental heterogeneity of the refugium. The deeply incised landscape of northern Idaho may have provided sufficient microclimatic variation to support spatially restricted refugia on south-facing aspects and at lower elevations than current mesic habitats (Daubenmire, 1975). Downscaling of palaeoclimate simulations and reconstructions may help evaluate topographic refugia during the last glacial maximum.

CONCLUSIONS

The high level of disequilibrium of species ranges with climate in the inland-glaciated area is significant for understanding biogeographical consequences of climate change. Several lines of evidence support the long-term existence of the Clearwater Refugium and its contribution to a local diversity hotspot. Such locations potentially function as predispersed nuclei to aid migration during climate change (Sala *et al.*, 2000). However, the cluster analysis and the restriction of many coastal disjunct species to inland-glaciated areas suggest that the coastal sources were as important as the Clearwater Refugium for post-glacial range expansion. It is likely that a combination of dispersal potential (both over large barriers and within continuous habitat), establishment success and fecundity has controlled colonization of glaciated habitats.

The biogeographical responses of vascular plant species to future climate change in highly fragmented habitat may not closely follow climate. A disequilibrium between species distributions and climate, as currently exists for the inland coastal-disjunct species for the Pacific Northwest, may persist for long periods, raising the importance of extinction on the trailing edge of distributions. As shown in this study by the success of certain species in colonizing remote inland-glaciated areas, species traits play a critical role in evaluating the threat of changing climate on extinction. To further reveal the complexity of biogeographical responses to climate change on a heterogeneous landscape, a successful approach is likely to require merging several sources of data and analyses (modern distributions, phylogeography and palaeorecords) and comparing results among a set of species with important differences in life-history traits. Such an approach is likely to provide a mechanistic understanding for the individualistic responses of species to climate change observed in palaeorecords.

ACKNOWLEDGEMENTS

This study was developed from a paper presented in the symposium ‘Forecasting future ecosystem states in a time of global change: from models to management’ at the 2008 Annual Meeting of the Ecological Society of America in Milwaukee, WI. I thank *P.J. Bartlein* and *F.S. Hu* for discussions regarding many of the ideas in this study. I thank *E. Herring*, *M. Konradi*, *M. Walsh* and *I.D. Crickmore* for comments on early versions of the manuscript, and *A. Boyer* and two anonymous referees for detailed reviews.

REFERENCES

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, R.S. & Whitlock, C.

(1998) Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. *Quaternary Science Reviews*, **17**, 549–585.

Blinnikov, M., Busacca, A. & Whitlock, C. (2002) Reconstruction of the late Pleistocene grassland of the Columbia basin, Washington, USA, based on phytolith records in loess. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **177**, 77–101.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J. & Stockwell, D.R.B. (2007) Forecasting the effects of global warming on biodiversity. *BioScience*, **57**, 227–236.

Brunelle, A. & Whitlock, C. (2003) Postglacial fire, vegetation, and climate history in the Clearwater Range, Northern Idaho, USA. *Quaternary Research*, **60**, 307–318.

Brunsfeld, S.J. & Sullivan, J. (2005) A multi-compartmented glacial refugium in the northern Rocky Mountains: evidence from the phylogeography of Cardamine constancei (Brassicaceae). *Conservation Genetics*, **6**, 895–904.

Brunsfeld, S.J., Sullivan, J., Soltis, D.E. & Soltis, P.S. (2001) Comparative phylogeography of northwestern North America: a synthesis. *Integrating ecological and evolutionary processes in a spatial context* (ed. by J. Silvertown and J. Antonovics), pp. 319–339. Blackwell Science, Oxford.

Brunsfeld, S.J., Miller, T.R. & Cartstens, B.C. (2007) Insights into the biogeography of the Pacific Northwest of North America: evidence from the phylogeography of *Salix melanopsis*. *Systematic Botany*, **32**, 129–139.

Cain, M.L., Damman, H. & Muir, A. (1998) Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs*, **68**, 325–347.

Carstens, B.C., Stevenson, A.L., Degenhardt, J.D. & Sullivan, J. (2004) Testing nested phylogenetic and phylogeographic hypotheses in the Plethodon vandykei species group. *Systematic Biology*, **53**, 781–792.

Carstens, B.C., Brunsfeld, S.J., Demboski, J.R., Good, J.M. & Sullivan, J. (2005) Investigating the evolutionary history of the Pacific Northwest mesic forest ecosystem: Hypothesis testing within a comparative phylogeographic framework. *Evolution*, **59**, 1639–1652.

Chase, M., Bleskie, C., Walker, I.R., Gavin, D.G. & Hu, F.S. (2008) Midge-inferred Holocene summer temperatures in Southeastern British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **257**, 244–259.

Chatters, J.C. & Leavell, D. (1994) *Smeads Bench Bog: a 1500 year history of fire and succession in the hemlock forest of the lower Clark Fork valley, Northwest Montana*. Report prepared for the Kootenai National Forest, Libby, MT. Contract number RFQ 14-93-05.

Cooper, S.V., Neiman, K.E. & Roberts, D.W. (1991) *Forest habitat types of northern Idaho: a second approximation*. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Cowling, S.A. & Sykes, M.T. (1999) Physiological significance of low atmospheric CO2 for plant-climate interactions. *Quaternary Research*, **52**, 237–242.

Currie, D.J. (1991) Energy and large-scale patterns of animal-species and plant-species richness. *The American Naturalist*, **137**, 27–49.

Currie, D.J. (2007) Disentangling the roles of environment and space in ecology. *Journal of Biogeography*, **34**, 2009–2011.

Daly, C., Neilson, R.P. & Phillips, D.L. (1994) A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology*, **33**, 140–158.

Daubenmire, R.F. (1952) Plant geography of Idaho. *Flora of Idaho* (ed. by R.J. Davis), pp. 1–17. WM. C. Brown Company, Dubuque, IA.

Daubenmire, R.F. (1956) Climate as a determinant of vegetation distribution in eastern Washington and northern Idaho. *Ecological Monographs*, **26**, 131–154.

Daubenmire, R.F. (1975) Floristic plant geography of eastern Washington and northern Idaho. *Journal of Biogeography*, **2**, 1–18.

Douglas, G.W. (1996) Endemic vascular plants of British Columbia and immediately adjacent regions. *The Canadian Field – Naturalist*, **110**, 387–389.

Dyke, A.S., Moore, A. & Robertson, L. (2003) *Deglaciation of North America*. Geological Survey of Canada Open File 1574. Natural Resources Canada, Ottawa.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Frenkel, R.E. (1974) An isolated occurrence of Alaska-Cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) in the Aldrich Mountains, Central Oregon. *Northwest Science*, **48**, 29–37.

Gavin, D.G. & Hu, F.S. (2006) Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. *Journal of Biogeography*, **33**, 1384–1396.

Gavin, D.G., Hu, F.S., Walker, I.R. & Westover, K. (2009) The northern inland temperate rainforest of British Columbia: old forests with a young history? *Northwest Science*, **83**, 70–78.

Good, J.M. & Sullivan, J. (2001) Phylogeography of the red-tailed chipmunk (*Tamias ruficaudus*), a northern Rocky Mountain endemic. *Molecular Ecology*, **10**, 2683–2695.

Goward, T. & Spribille, T. (2005) Lichenological evidence for the recognition of inland rain forests in western North America. *Journal of Biogeography*, **32**, 1209–1219.

Hansen, H.P. (1955) Postglacial forests in south central and central British Columbia. *American Journal of Science*, **253**, 640–658.

Heinrichs, M.L., Hebda, R.J., Walker, I.R. & Palmer, S.L. (2002) Postglacial paleoecology and inferred paleoclimate in the Engelmann spruce-subalpine fir forest of south-central British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **184**, 347–369.

Higgins, P.A.T. & Harte, J. (2006) Biophysical and biogeochemical responses to climate change depend on dispersal and migration. *BioScience*, **56**, 407–417.

Jennings, M.D., Williams, J.W. & Stromberg, M.R. (2005) Diversity and productivity of plant communities across the Inland Northwest, USA. *Oecologia*, **143**, 607–618.

Johnson, F.D. & Steele, R. (1978) New plant records for Idaho from Pacific coastal refugia. *Northwest Science*, **52**, 205–211.

Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325–333.

Little, E.L., Jr (1971) *Atlas of United States trees, volume 1, conifers and important hardwoods*. U.S. Department of Agriculture Miscellaneous Publication v. 1146, 200 maps, Washington, DC.

Lorain, C.C. (1988) *Floristic history and distribution of coastal disjunct plants of the northern Rocky Mountains*. MS Thesis, University of Idaho, Moscow, ID.

McDowall, R.M. (2004) What biogeography is: a place for process. *Journal of Biogeography*, **31**, 345–351.

McGlone, M.S. (1996) When history matters: scale, time, climate and tree diversity. *Global Ecology and Biogeography Letters*, **5**, 309–314.

McLachlan, J.S. & Clark, J.S. (2004) Reconstructing historical ranges with fossil data at continental scales. *Forest Ecology and Management*, **197**, 139–147.

McLachlan, J.S., Clark, J.S. & Manos, P.S. (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, **86**, 2088–2098.

Mehringer, P.J., Jr (1996) *Columbia River Basin ecosystems: late Quaternary environments*. Interior Columbia Basin Ecosystem Management Project, (ICBEMP) Report, 91 pages. Available at: http://www.icbemp.gov/science/mehringe.pdf (last accessed 23 July 2009).

Montoya, D., Rodriguez, M.A., Zavala, M.A. & Hawkins, B.A. (2007) Contemporary richness of holarctic trees and the historical pattern of glacial retreat. *Ecography*, **30**, 173–182.

Nielson, M., Lohman, K. & Sullivan, J. (2001) Phylogeography of the tailed frog (*Ascaphus truei*): implications for the biogeography of the Pacific Northwest. *Evolution*, **55**, 147–160.

O'Connell, L.M., Ritland, K. & Thompson, S.L. (2008) Patterns of post-glacial colonization by western redcedar (*Thuja plicata*, Cupressaceae) as revealed by microsatellite markers. *Botany*, **86**, 194–203.

Otto-Bliesner, B.L., Brady, E.C., Clauzet, G., Tomas, R., Levis, S. & Kothavala, Z. (2006) Last glacial maximum and Holocene climate in CCSM3. *Journal of Climate*, **19**, 2526–2544.

Peery, R.M. (2005) *Postglacial recolonization of western hemlock (Tsuga heterophylla (Raf.) Sarg)*. M.S. Thesis Central Washington University, Ellensburg, WA.

Pellatt, M.G., Smith, M.J., Mathewes, R.W. & Walker, I.R. (1998) Palaeoecology of postglacial treeline shifts in the northern Cascade Mountains, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **141**, 123–138.

Proches, S. (2005) The world's biogeographical regions: cluster analyses based on bat distributions. *Journal of Biogeography*, **32**, 607–614.

Richardson, B.A., Brunsfeld, J. & Klopfenstein, N.B. (2002) DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). *Molecular Ecology*, **11**, 215–227.

Rosenberg, S.M., Walker, I.R. & Mathewes, R.W. (2003) Postglacial spread of hemlock (Tsuga) and vegetation history in Mount Revelstoke National Park, British Columbia, Canada. *Canadian Journal of Botany*, **81**, 139–151.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Biodiversity – global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Soltis, D.E., Mayer, M.S., Soltis, P.S. & Edgerton, M. (1991) Chloroplast-DNA variation in Tellima grandiflora (Saxifragaceae). *American Journal of Botany*, **78**, 1379–1390.

Soltis, D.E., Soltis, P.S., Kuzoff, R.K. & Tucker, T.L. (1992) Geographic structuring of chloroplast DNA genotypes in *Tiarella trifoliata* (Saxifragaceae). *Plant Systematics and Evolution*, **181**, 203–216.

Soltis, D.E., Gitzendanner, M.A., Strenge, D.D. & Soltis, P.S. (1997) Chloroplast DNA intraspecific phylogeography of plants from the Pacific Northwest of North America. *Plant Systematics and Evolution*, **206**, 353–373.

Steele, C.A., Carstens, B.C., Storfer, A. & Sullivan, J. (2005) Testing hypotheses of speciation timing in *Dicamptodon copei* and *Dicamptodon aterrimus* (Caudata: Dicamptodontidae). *Molecular Phylogenetics and Evolution*, **36**, 90–100.

Stewart, J.R. & Lister, A.M. (2001) Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology and Evolution*, **16**, 608–613.

Strenge, D. (1994) *The intraspecific phylogeography of Polystichum munitum and Alnus rubra*. MS Thesis, Washington State University, Pullman, WA, USA.

Svenning, J.C. & Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters*, **7**, 565–573.

Thackray, G.D., Lundeen, K.A. & Borgert, J.A. (2004) Latest Pleistocene alpine glacier advances in the Sawtooth Mountains, Idaho, USA: reflections of midlatitude moisture transport at the close of the last glaciation. *Geology*, **32**, 225–228.

Thompson, R.S., Whitlock, C., Bartlein, P.J., Harrison, S.P. & Spaulding, W.G. (1993) Climatic changes in the western United States since 18,000 years BP. *Global climates since the last glacial maximum* (ed. by H.E. Wright Jr, J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-perrott and P.J. Bartlein), pp. 468–513. University of Minnesota Press, Minneapolis, MN.

Wang, T., Hamann, A., Spittlehouse, D.L. & Aitken, S.N. (2006) Development of scale-free climate data for western Canada for use in resource management. *International Journal of Climatology*, **26**, 383–397.

Whitlock, C. (1992) Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present day biodiversity. *Northwest Environmental Journal*, **8**, 5–28.

Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

Willmott, C.J., Rowe, C.M. & Mintz, Y. (1985) Climatology of the terrestrial seasonal water cycle. *Journal of Climatology*, **5**, 589–606.

SUPPORTING INFORMATION

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

Appendix S1 A list of tree and understorey species included in the analyses.

BIOSKETCH

Daniel G. Gavin is an Assistant Professor of Geography, University of Oregon, with interests in biogeographic responses to climate change and forest disturbance during the Holocene. He specializes in the biogeographic implications of changing fire regimes in western North America.

Editor: George Stevens