Research

Climate refugia and migration requirements in complex landscapes

David R. Roberts and Andreas Hamann

D. R. Roberts (drr3@ualberta.ca) and A. Hamann, Dept of Renewable Resources, Univ. of Alberta, 751 General Services Building, Edmonton, AB T6G 2H1, Canada. DRR also at: Dept of Biometry and Environmental System Analysis, Univ. of Freiburg, DE-79106 Freiburg, Germany.

All of today's species have proven their ability to cope with climate change during the glacial-interglacial cycles of the Quaternary, but future migration requirements may be different regarding speed, direction, geographic barriers, and availability of nearby climate refugia. Here, we contribute a landscape-level climatic analysis of postglacial vs. projected future migration requirements for 24 common western North American tree species. Using a recently developed velocity of climate change algorithm, we quantify required migration velocities for all populations of species to track climate habitat, based on projections from general circulation models for the 2080s and the last glacial maximum, 21 000 yr ago. Specifically, we ask if nearby climate refugia exist for at least some populations within species ranges and whether the current landscape position of species imply qualitatively different migration requirements in the future compared to those during glacial-interglacial cycles. Results showed that velocities to reach the nearest climate refugia in the future still exceed the fastest reconstructed post-glacial migration requirements, but not by orders of magnitude. Regarding landscape positions, we find a low correlation among past and future migration requirements ($r = 0.38$), suggesting that qualitatively different migration patterns may emerge in the future for some species. Species identified as occupying landscape positions requiring disproportionally faster migration requirements in the future include whitebark pine, pinyon pine, and coast redwood. We discuss uncertainties of our analytical approach as well as implications for human-assisted migration and conservation action to address climate change.

All present day species have demonstrated their ability to cope with climatic change associated with glacial-interglacial oscillations of the past either through genetic adaptation, migration, environmental tolerances, or a combination of these factors. This does not, of course, imply the maintenance of all germplasm of species, as many locally adapted populations may have been extirpated through recurring population bottlenecks of the Pleistocene (Hewitt 2004). However, the apparent lack of widespread extinctions through the last glaciations suggests a general capability of species to migrate or adapt in response to landscape-level environmental change (Botkin et al. 2007).

Future migration requirements may, however, be notably different than postglacial migration requirements for several reasons. First, future change is projected towards climates that have not existed for millions of years (Crowley 1990). Second, species may encounter different geographic constraints to migration, such as human land use (García-Valdés et al. 2015). Third, topographically complex landscapes will produce great variation in rates of movements of suitable species habitat under climate change (Loarie et al. 2009, Diffenbaugh and Field 2013, Dobrowski et al. 2013b) and the arrangement and availability of climate refugia in the future may be different than in the past (Gavin et al. 2014). Finally, past patterns of climate change had large regional and temporal variation, including localised, abrupt climate

change events (Alley et al. 2003). Thus, the persistence of the species as a whole also does not imply that all local populations, subject to rapid regional climate changes, were able to survive.

The capacity of species to migrate in response to past climate change have been inferred from where and when species appear in the palaeoecological record (Davis 1981, Huntley and Birks 1983, Delcourt and Delcourt 1987, King and Herstrom 1997, Gugger and Sugita 2010, Ordonez and Williams 2013a). However, such approaches are limited by a scarcity of fossil records and cryptic glacial refugia, which could result in overestimates of migration capability assessments (McLachlan et al. 2005, Snell and Cowling 2015). An alternative approach is to estimate past expansion rates based on species distribution models paired with reconstructions of palaeoclimates (Davis 1989, Davis and Zabinski 1992, Schwartz 1992, Iverson and Prasad 2002, Malcolm et al. 2002, Meier et al. 2012, Ordonez and Williams 2013a). Such models assume that all populations within a species range can occupy the entire realised niche of the species, but genetic adaptation to different environments within a species range do, in fact, impose additional constraints (Davis and Shaw 2001).

For locally adapted populations to persist through environmental change, they must adapt, migrate, or face local extirpation (Aitken et al. 2008). In common and widespread

tree species, much of the adaptive response to changing environments may be achieved through pollen flow rather than seed dispersal or genetic change through mutation and selection. In landscape positions such as regions of high topographic and climatic diversity with steep environmental gradients, populations may find either nearby genetic source material required for adaptation to new environments, or emerging new habitat analogue to past conditions in the immediate vicinity (i.e. climate refugia). In contrast, populations occupying large plateaus or plains may be required to either source necessary genetic material from distant populations or find suitable future climate refugia farther afield (Ackerly et al. 2010).

To better quantify migration requirements across different types of landscapes, Loarie et al. (2009) introduced the concept of 'velocity of climate change' to describe an initial speed and direction at which species must migrate over the surface of the earth to maintain constant climate conditions. Their approach has been employed to evaluate the integrity of protected area systems under climate change (Ackerly et al. 2010, Schueler et al. 2014), to describe the expected rate and direction of climate migrants (Dobrowski et al. 2013a , Burrows et al. 2014), to identify climate refugia during glacial-interglacial cycles (Sandel et al. 2011), and to assess whether eastern North American species were able to track changing climate conditions of the past (Ordonez and Williams 2013a). However, the metric only provides an initial measure of local velocity based on climate differences between a specific site and its immediate surroundings. The analysis provides neither information on suitable future destinations for populations, nor on the proximity of suitably adapted source populations that could occupy newly available habitat under climate change.

To address these issues, variants of the initial velocity metrics have been developed that measure distances between analogous climate arrangements in alternative time periods (see comparison by Carroll et al. 2015). Such approaches developed by Ordonez and Williams (2013b) and Hamann et al. (2015) measure distances from a current position in the landscape to the nearest site with analogous climate predicted in the future or past, akin to classifying suitable habitats in species distribution models (Chen 2015). However, results are independently calculated and reported for each individual grid cell of a landscape rather than for the inferred climate niche space of a species. Such velocity metrics can identify local climate refugia (i.e. nearby climate equivalents) for populations as well as vulnerable topographic positions (e.g. mountaintops and plains) where long-distance migrations may be required, making this velocity-based approach more suitable for finer scale analysis and applications in conservation and management (Hamann et al. 2015).

In this study, we apply a landscape-level climate analogue analysis within current species ranges and their projected climate habitats based on general circulation model projections. We compare the distributions of simulated postglacial and future migration requirements within species ranges for populations of 24 western North American tree species. In doing so, we identify climate refugia but also disproportionately large challenges to migration under projected climate change. Specifically, we test two working hypotheses. First, we expect that for at least some populations in complex landscapes, analogue climate habitat should be nearby and well within migration requirements of the past, thus indicating relative safety under projected climate change. Second, we expect that some species had nearby climate refugia during glacial oscillations (e.g. by populations on elevation gradients migrating up- and down-slope). However, their current position on the landscape (e.g. near mountain-tops) may not provide nearby climate refugia in the future, making those species disproportionately vulnerable to climate change. We discuss our results in terms of implications for prioritising human-assisted migration and conservation action to address climate change.

Methods

Past, present, and future climate data

All climate data representing current, past, and future periods were generated with the ClimateWNA ver. 4.72 software package, which is available for download under the permanent link <http://tinyurl.com/ClimateWNA> (Hamann et al. 2013). The software overlays future projections and hindcasts from general circulation models (GCMs) on high-resolution climate normal data, applying lapse-rate-based elevation adjustments to improve the accuracy of climate surfaces. We used ten GCM projections for the last glacial maximum 21 000 yr ago, made available through the National Oceanic and Atmospheric Administration (NOAA): BMRC2, CCM1, CCSR1, ECHAM3, GEN2, GFDL, LMD5, MRI2, UGAMP, and UKMO (Braconnot et al. 2007). Future climate projections for the 2071–2100 period, hereafter referred to as the 2080s, were based on A2 emissions scenarios implemented by 14 GCMs of the CMIP3 multi-model dataset: BCCR-BCM2.0, CCSM3.0, CGCM3.1 (T63), CNRM-CM3, CSIRO-Mk3.0, ECHAM5/MPI-OM, ECHO-G, GFDL-CM2.1, GISS-ER, INM-CM3.0, IPSL-CM4, MRI-CGCM2.3.2, PCM1, and UKMO-HadCM3, referenced in the IPCC's Fourth Assessment Report (IPCC 2007). To represent current climate conditions, we use interpolated weather station data for the 1961–1990 normal period generated with PRISM methodology (Hamann et al. 2013).

Gridded climate surfaces for ten biologically relevant climate variables were generated in Lambert Conformal Conic projection at 1 km resolution (subsampled at 4 km resolution for analysis). The variables included mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, the difference between the mean warmest and mean coldest month temperatures as a measure of continentality, mean annual precipitation, growing season precipitation from May to September, the number of growing degree days above 5°C, the number of frost-free days, and annual and summer heat moisture indices. Details on interpolation methods and estimation of variables are available in Wang et al. (2012).

Forward and reverse migration requirements

Climate change velocities were calculated with algorithms provided by Hamann et al. (2015). For each grid cell in a

reference climate data set (past, present, or future), all grid cells with equivalent climates in the alternative data set were identified and the geographic distance to the closest cell was recorded. Velocities were obtained by dividing these distances by the number of interim years (e.g. 21 000 yr between the last glacial maximum and the 1961–1990 normal period; 110 yr between the 1961–1990 normal period and the 2080s period). Because many climate variables are highly correlated, multivariate climate analogues were based on the first two components from a principal component analysis of the pooled climate data (accounting for 51 and 38% of the total variance in original climate variables, respectively). Reference climate surfaces for the first component were divided into 120 equal width classes and the second component was then assigned to classes with identical width. Because not all combinations of the first two principal components are represented in the data, this resulted in approximately 5000 unique climate combinations. Matching climates were considered to be those within the same unique multivariate climate bin. Hamann et al. (2015) demonstrated that, while increasing or decreasing the number of bins linearly changes absolute calculated distances, general landscape patterns stay consistent and allow for robust relative comparisons of vulnerabilities of populations due to landscape position. Generic univariate and multivariate velocity grids for western North America are available for public download under the permanent link <http://tinyurl.com/VelocityWNA> (Hamann et al. 2015).

Code to implement forward and reverse distance and velocity calculations within the R programming environment (R Core Team) are provided as appendices to Hamann et al. (2015). Velocity calculations were made in both directions (forward and reverse) for each of the 14 future projections and 10 hindcasts from GCMs. We subsequently calculated the mean velocity across all future projections or across all hindcast runs.

Projected and reconstructed species habitats

To summarise migration requirements at the species level, the method was applied to pairs of modelled species ranges (projections for different time periods). Because both the modelled species ranges and the velocity calculation are defined by matching climate conditions (Chen 2015, Hamann et al. 2015), a cell outside the modelled species climate niche as a candidate for velocity calculations cannot be a close climate match to another cell within the niche, making the velocity analysis largely independent of the modelled species ranges. We do, however, use the modelled ranges to distinguish migration requirements that can be met through pollen flow (overlapping portions of range projections) and those that require seed dispersal (non-overlapping portions).

The future projections and hindcasts of species ranges were previously developed and validated (Roberts and Hamann 2012, 2015). Briefly, species distribution model projections were based on an ensemble approach, incorporating three class-based statistical models, trained with North American forest inventory data paired with the 1961–1990 normal climate data (Roberts and Hamann 2012). We assessed model fit with a random cross-validation of model training data, using the area under the curve of the receiver operating characteristic (AUC), resulting in an average AUC of 0.92 ($\sigma = 0.05$) across species. Because cross-validations with random data splits can result in optimistic validation statistics due to autocorrelations (Araújo et al. 2005), we also performed a validation using a spatial data split, resulting in an average AUC of 0.86 ($\sigma = 0.13$) across species. Last, we performed a validation against pooled palaeoecological data from various past periods since the last glacial maximum, resulting in an average AUC of 0.71 ($\sigma = 0.10$) across species, a value in line with other independent model validations in the literature (Heikkinen et al. 2012, Eskildsen et al. 2013). We also provide here a visual comparison of modelled species ranges from the last glacial maximum with fossil pollen and macrofossil records from the last glacial maximum (Supplementary material Appendix 1, Fig. A1), as well as a comparison of forward postglacial velocities calculated from modelled ranges with those calculated from fossil record presence points (Supplementary material Appendix 1, Fig. A2), though for the glacial period at 21 000 yr ago, most tree species considered in this analysis have very few or no presence records in the palaeoecological data within our study area.

Results

In maps and other summaries of migration requirements (distances to analogous habitat) using histograms and plots, we can differentiate between overlapping and non-overlapping habitat projections. Distances for non-overlapping habitat areas represent migration-by-dispersal requirements, while distances to analogous climates within overlapping habitat represent pollen or gene flow requirements that would allow genetically differentiated populations in wide ranging species to adapt to new climate environment. However, unless otherwise stated, we consider both types (dispersal and gene flow) together under the term 'migration requirements'. Here, we use the example of *Pinus ponderosa* (ponderosa pine, Fig. 1) to describe these mapped patterns in more detail. Mapped migration requirements for all 24 considered species for past and future calculations are provided in Supplementary material Appendix 1, Fig. A3–A26.

Migration requirements to nearest climate equivalent

In maps of migration requirements from the current distribution back to the last glacial maximum (Fig. 1a), the colours indicate calculated distances that modern populations were required to move (through gene flow or migration) from analogous climate habitats 21 000 yr ago. Reconstructed migration requirements are higher (1500 km or more) for the northern edges of the current distribution while requirements for the southern montane populations of today's species range are lower (e.g. 200 km or less for the Arizona/New Mexico Mountains). These current populations have nearby analogues at lower elevation in the climate reconstructions of the last glacial maximum (dark-grey areas surrounding today's montane populations in green).
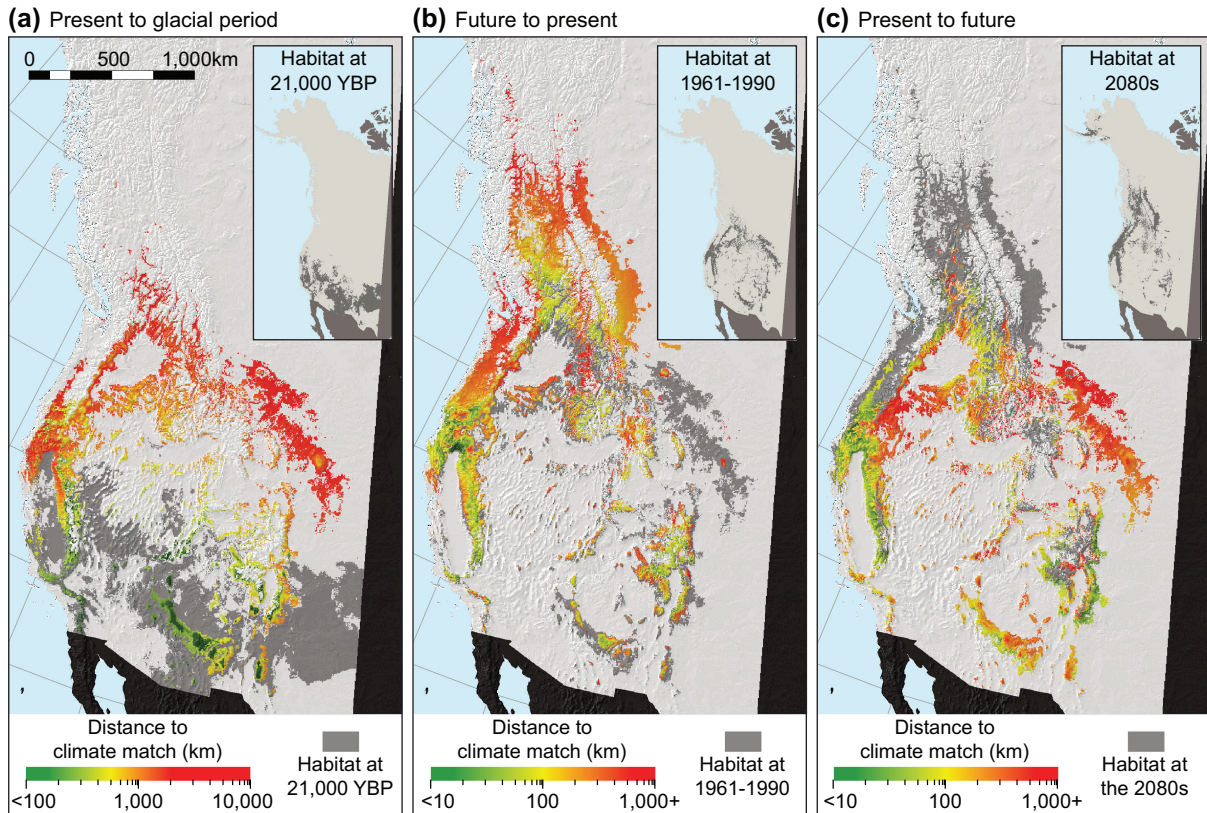
Figure 1. Distances to the nearest analogous climate for *Pinus ponderosa* (ponderosa pine) for the past and future. Distance are calculated (a) in reverse from the 1961–1990 climate normal period the last glacial maximum 21 000 yr ago, representing postglacial migration requirements, (b) in reverse from projected climate for the 2080s period to the 1961–1990 normal period, representing future migration requirements to fill available habitat, and (c) forward from the 1961–1990 normal period to the 2080s, representing the distance that current populations must travel to reach future climate equivalents. Maps for all species are provided in Supplementary material Appendix 1.

The equivalent calculation for the future (Fig. 1b) shows similar patterns, with the highest migration requirements in the most northern portions of the distribution. Note that the geographic distance between future coastal habitat and current populations in the interior east of the Cascade Mountains may be small, but those populations do not constitute a matching climate and are therefore not considered a plausible climate refugium by the velocity analysis. In the southern range areas, projected climate refugia are at higher elevation (e.g. green patches upslope in the Arizona/New Mexico Mountains). However, the extent of climate refugia is much smaller than for the measurement between the present and the last glacial maximum (Fig. 1a versus 1b).

The forward distance calculation into the future (Fig. 1c) represents how far present-day populations would have to migrate (either through dispersal or gene flow) to find analogous climate habitat in the future. In the southern interior mountain ranges of Arizona and New Mexico, the low elevation bands, especially on southern slopes, show short required migration distances (green and yellow) to suitable climate habitat up-slope. The populations near the mountaintops, however, have no nearby climate equivalents in the projected future (red). Although this high-velocity portion of the range is not predicted to be lost to the species (green areas in Fig. 1b), locally adapted genotypes in those mountain top positions may be extirpated through replacement with

better-adapted genotypes from down-slope. Thus, the forward and reverse measurements complement each other in identifying climate change vulnerabilities. The forward calculation (Fig. 1c) identifies the potential loss of locally adapted populations for lack of nearby climate refugia, while the reverse calculation (Fig. 1b) identifies migration requirements to appropriately occupy future climate habitats.

Past versus future migration requirements

For all species, the fastest (95th percentile) postglacial migration requirements ($\sim$ 50–200 m yr^{-1}) exceed the slowest (5th percentile) future migration requirements ($\sim$ 300–1600 m yr^{-1}), but not by several orders of magnitude (factors within species of 2.5$\times$ to 20$\times$). Distribution statistics for 5th percentile, median, and 95th percentile required migration distance and velocity values for each species analysed in this study are provided as Supplementary material Appendix 2, Table A1 (distances) and Table A2 (velocities). Figure 2 shows frequency distributions of required migration distances for projected future (red) and reconstructed postglacial (blue) periods. The histograms have been aligned to the median across all species (vertical line) to better demonstrate relative changes in the migration requirements among species or species groups. For example, boreal species (no. 14–18)

Mesic: coastal only

1. *Abies amabilis*
   (Pacific silver fir)
2. *Abies procera*
   (noble fir)
3. *Acer macrophyllum*
   (bigleaf maple)
4. *Alnus rubra*
   (red alder)
5. *Calocedrus decurrens*
   (incense cedar)
6. *Cupressus nootkatensis*
   (yellow cedar)
7. *Picea sitchensis*
   (Sitka spruce)
8. *Sequoia sempervirens*
   (coast redwood)

Mesic: coastal & interior

9. *Pinus monticola*
   (western white pine)
10. *Pseudotsuga menziesii*
    (Douglas-fir)
11. *Thuja plicata*
    (western redcedar)
12. *Tsuga heterophylla*
    (western hemlock)
13. *Tsuga mertensiana*
    (mountain hemlock)

Boreal & sub-boreal

14. *Betula papyrifera*
    (paper birch)
15. *Picea glauca*
    (white spruce)
16. *Picea mariana*
    (black spruce)
17. *Pinus contorta*
    (lodgepole pine)
18. *Populus temuloides*
    (trembing aspen)

Sub-alpine

19. *Abies lasiocarpa*
    (sub-alpine fir)
20. *Picea engelmannii*
    (Engelmann spruce)
21. *Pinus albicaulis*
    (whitebark pine)

Xeric & sub-xeric

22. *Larix occidentalis*
    (western larch)
23. *Pinus edulis*
    (pinyon pine)
24. *Pinus ponderosa*
    (ponderosa pine)

Present to 2080s: 2   8   32   128   512   2,048
Present to glacial period: 2   8   32   128   512   2,048
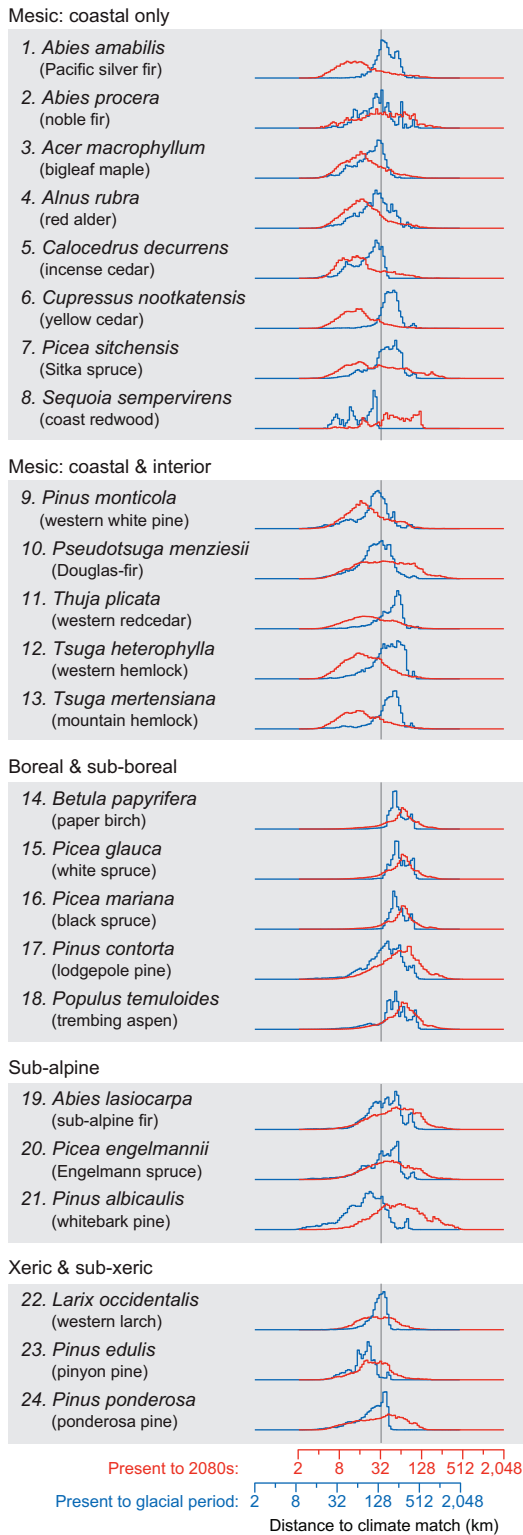Distance to climate match (km)

Figure 2. Frequency distributions of migration requirements to nearest climate equivalents for the past and future. Reverse measurements, representing postglacial migration requirements (blue), compared to forward measurements, representing migration requirements to future climate refugia (in red). Past and future histograms have been aligned to the average median distance across all species (vertical line) to facilitate the comparison of the shapes of distributions, as absolute magnitudes vary greatly. Refer to Supplementary material Appendix 2 for additional data corresponding to this figure.

in both the past and future tend to have the longest migration requirements, as indicated by distributions right of the median. Coastal species (no. 1–8) have short overall migration requirements, and relatively shorter future than past requirements. Many of these species, such as *Abies amabilis* (Pacific silver fir, no. 1) and *Cupressus nootkatensis* (yellow cedar, no. 6), exhibit notable changes in distribution shapes, with future distributions shifted to the left, indicating a general positioning on the landscape with a larger proportion of nearby analogous future climates. Conversely, future migration requirements for species such as *Sequoia sempervirens* (coast redwood, no. 8) and *Pinus albicaulis* (whitebark pine, no. 21) tend to be higher relative to other species, suggesting that such species occupy geographic position on the landscape with fewer nearby climate analogues in the projected future.

We interpret the lowest (5th percentile) distances to the nearest climate refugia in the reconstructed past and projected future to represent the minimum migration requirements to ensure survival at the species level. Among species, we find a moderately strong positive relationship between the past and the future requirements (r = 0.67; Fig. 3a). Nearby climate refugia in the past were most readily available for coastal species and least available to boreal species, and the same appears to be true in future projections. Moderate deviations above the diagonal include *Picea glauca* (white spruce, no. 15) and *Larix occidentalis* (western larch, no. 22), suggesting that some populations of these species are relatively closer to future climate refugia than analogues in past climate reconstructions. Species with somewhat lower availability of future climate refugia than in the past include *Sequoia sempervirens* (coast redwood, no. 8), *Pinus contorta* (lodgepole pine, no. 17), and *Populus tremuloides* (trembling aspen, no. 18), positioned below the diagonal in Fig. 3a.

Figure 3b shows the median distances to climate matches, measured in reverse, for the past (present to glacial period) and future (2080s to present) periods, representing typical migration requirements to colonise newly available habitat. For this metric, the correlation between the past and the future is weaker (r = 0.38; Fig. 3b), indicating that many species will encounter qualitatively different migration patterns to colonise newly available habitat in the future than in the past. Species falling to the upper-left in this plot, e.g. *Cupressus nootkatensis* (yellow cedar, no. 6), tend to have emerging habitat in future projections that is relatively closer to colonisation sources (represented by the current distribution). For species positioned in the bottom-right, including *Sequoia sempervirens* (coast redwood, no. 8) and *Pinus albicaulis* (whitebark pine, no. 21), future habitat is farther removed from potential colonisation sources than in the past reconstructions.

As an overall assessment of risk for locally adapted populations within species, Fig. 3c shows for which portion of the range migration of genotypes can be facilitated by pollen flow (overlap between present-day and projected future habitat) and the median distances of required pollen flow within the area of range overlap (based on a reverse calculation). In this figure, species in the upper left have little overlap between their present and projected future ranges and the gene flow within this overlap must overcome large distances to reach suitable climate habitats. Conversely,
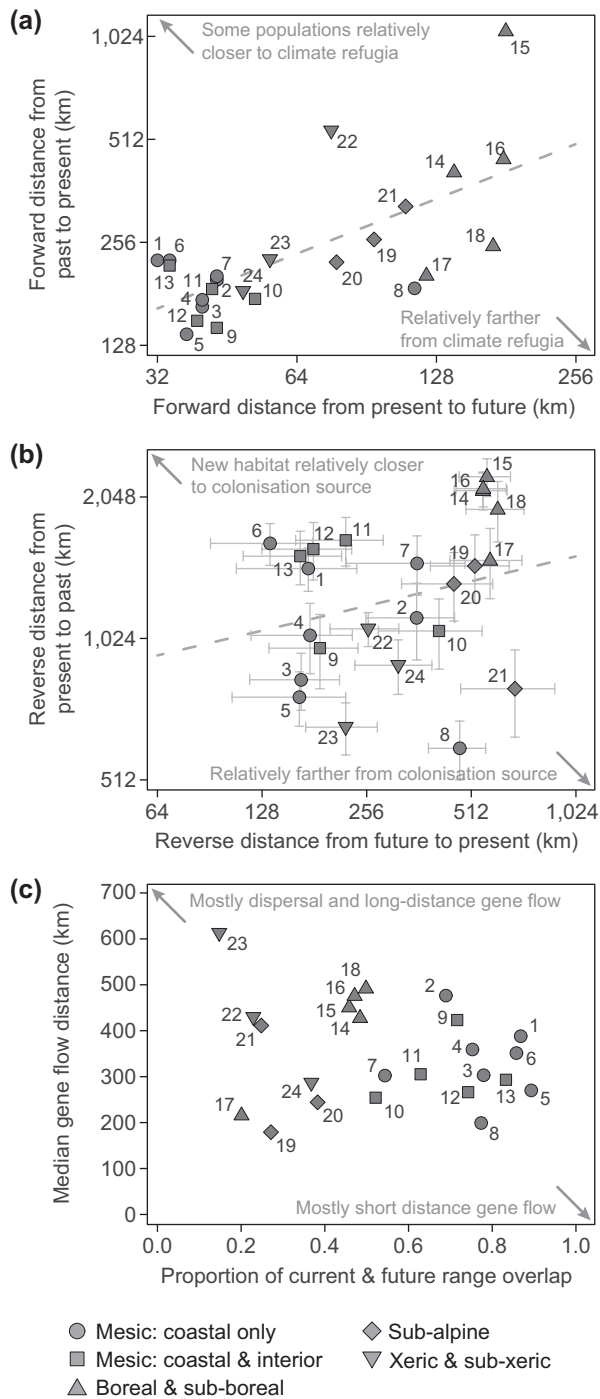
(a)

(b)

(c)

Figure 3. Relationships between required migration and gene flow distances for the past and future, showing (a) availability of climate refugia represented by forward distances of the 5th percentile of populations nearest to a climate equivalent; (b) typical migration requirements to occupy new habitat in the past versus future, represented by average reverse distances with bars representing standard error across GCMs; and (c) a breakdown of future migration versus gene-flow requirements comparing the proportion of the present and future species range overlap with the median distance required therein. Numbers on plots correspond to species listed in Fig. 2. Complete data for these graphs is provided in numerical format in Supplementary material Appendix 2.

present and future ranges for species in the lower right of the plot are mostly shared and suitably adapted genetic material therein can largely be sourced from nearby locations. Of the species falling towards the best case scenario (stable ranges, short gene flow distances), most are mesic species with either coastal (circles) or coastal and interior (squares) ranges. With the exception of *Pinus contorta* (lodgepole pine, no. 17), a widespread generalist, most boreal species (upward triangles) have moderate habitat overlap but require relatively long-distance gene flow. While species found in montane (diamonds) and xeric regions (downward triangles) show the lowest proportions of projected habitat overlap (implying the necessity of migration-by-dispersal), most gene flow requirements are low, suggesting that suitably adapted material may be sourced nearby. A notable outlier is *Pinus edulis* (pinyon pine, no. 23), which exhibits the smallest proportion of range overlap and the highest gene flow distances within that overlapping range.

Discussion

Availability of climate refugia

We initially hypothesised that the fastest postglacial migration requirements may exceed minimum future migration requirements to nearby climate refugia, indicating that at least some populations within the species range should not be threatened by climate change. However, for most of the tree species considered in this paper, maximum postglacial migration requirements exceed the minimum migration requirements to nearby climate refugia in the future (Supplementary material Appendix 2, p95/past/reverse versus p05/future/forward). However, this comparison assumes a constant rate of postglacial and future warming, which was and will almost certainly not be the case. As a less conservative estimate, if we assume that most postglacial warming occurred in the 5000 yr between ca 16 000 and 11 000 yr ago (Petit et al. 1999), results for reconstructed postglacial migration are approximately four times higher. Under this assumption, minimum future migration requirements (~ 300–1600 m yr^{-1}) only exceed the reconstructed maximum postglacial requirements for 16 of the 24 species (on average by a factor of 1.5×). In this scenario, future minimum (5th percentile) migration requirements for many species with coastal distributions fall under the postglacial maximums (95th percentile) (Supplementary material Appendix 2, p95/past/reverse (× 4) versus p05/future/forward).

Colonisation of new habitat

We also do not find general support for our second hypothesis that future migration requirements may be qualitatively different than postglacial migration requirements, as many species encounter different geographic constraints to occupying newly available habitat (Fig. 3b). While coastal species may find nearby climate refugia up-slope along the coast mountain cordilleras, the full occupation of newly available habitat requires migration along a narrow strip

of coastal habitat that is more demanding than in the past (Fig. 3b, most circles under the diagonal). *Sequoia sempervirens* (coast redwood) has the highest relative change in migration requirements in the future (Fig. 3b, no. 8 and Supplementary material Appendix 1, Fig. A21a versus b). Of the three subalpine species included in this study (Fig. 3b, no. 19–21), we find that only *Pinus albicaulis* (whitebark pine) occupies a landscape position today that appears qualitatively different. In the past, the species may have been capable of responding to glacial-interglacial fluctuations through local up- and down-slope migrations, with reconstructed glacial ranges occupying a much larger area of low-elevation landscape. Under projected warming, however, the current climate refugia for the species are predicted to shrink further (Fig. 3b, no. 21 and Supplementary material Appendix 1, Fig. A14a and A14b). Among the xeric species, *Pinus edulis* (pinyon pine) shows the largest discrepancy in colonisation distance between the past and future, most of which is predicted to require seed dispersal rather than gene flow (Fig. 3c, no. 23 and Supplementary material Appendix 1, Fig. A16 a and b). These examples highlight the considerable variation in future migration requirements to newly available habitat for individual species, emphasizing the need to prioritise where assisted migration prescriptions or other conservation measures are needed most.

Implications for gene conservation and assisted migration

For wide-ranging species that consist of locally adapted populations, landscape positions matter when considering climate change risks. Widely variable migration requirements within a single species are evident, for example, in maps of *Pinus ponderosa* (ponderosa pine; Fig. 1, Supplementary material Appendix 1, Fig. A18) and *Pseudotsuga menziesii* (Douglas-fir, Supplementary material Appendix 1, Fig. A20), where notable boundaries in migration requirements divide modern coastal and interior subspecies. This pattern is in contrast to species that expanded postglacially from a single refugium, which results in much more uniform migration requirements, such as *Picea sitchensis* (Sitka spruce; Supplementary material Appendix 1, Fig. A13) or *Thuja plicata* (western redcedar; Supplementary material Appendix 1, Fig. A22). Forward velocity calculations can thus be used to identify the vulnerability of locally adapted populations, e.g. to prioritise areas for ex-situ seed collections for gene conservation.

Our results also have implications for assisted migration or assisted gene flow prescriptions in reforestation programs to address climate change (Aitken et al. 2008). The distance from projected future climate equivalents back to observed modern ranges can be interpreted as a relative difficulty for populations to adapt to new climate conditions supported by gene flow from matching populations. A strategy of minimal intervention through human assisted migration would focus on populations of species where evolutionary adaptation to new climate conditions is not facilitated by gene flow from nearby populations. Because gene flow is generally high in wind-pollinated temperate tree species, populations with nearby climate equivalents may already contain appropriate genotypes, allowing for rapid genetic adaptation to new climate conditions. Conversely, some areas of overlap in projected present and future habitats, often interpreted as unproblematic regarding forest health and productivity, may require human intervention if climate conditions in these areas moves rapidly outside the tolerances of locally adapted genotypes. If there are no nearby current climate equivalents as indicted by reverse velocities, appropriate genotypes could be introduced through normal operations in reforestation programs (Gray et al. 2011).

While this study was conducted for western North American tree species, the approach is broadly suitable to assess the exposure of any species group to climate change in complex landscapes. For example, the approach could be combined with landscape resistance algorithms for faunal movement (Lawler et al. 2013) to find critical climate driven movement routes that avoid migratory traps in the landscape (such as mountain top positions) and minimise other migration barriers such as landscape fragmentation. Incorporating the methods presented here, the combination of species distribution model projections with a velocity algorithm provides more informative climate change vulnerability assessments than either approach alone. To prioritise where migration prescriptions are best targeted, we would suggest three criteria to be applied: 1) high rates of observed climate change, 2) high velocities as calculated in this study, partially driven by the climate change signal and partially driven by the landscape configuration, and 3) locally observed biological or ecological issues such as demographic declines or health and productivity issues.

Limitations of the analogue velocity approach

There are some important limitations for this climatic landscape analysis that should be kept in mind for applications in conservation and management that aim to address climate change issues. First, while the assumption that all populations of a species have the same climatic tolerances is certainly a critical flaw for many widespread tree species, this analysis makes an opposite assumption that is also not true. Namely, a search for analogue climate grid cells implies that each grid cell contains a 'local population' without climatic tolerances that must perfectly track its current climate space. In reality, locally adapted populations do not need to perfectly track their climate niche and do not need to be exactly pre-adapted to anticipated climate environments, thus relaxing migration requirements. Even for species with strong genetic structure, gene flow has likely reduced population differentiation, further reducing migration requirements. Last, 'migration requirements' reported in this study can at least partially be met through pollen flow in areas of range overlap, yet further easing migration requirements through seed dispersal. Therefore, the analogue velocity metric should not be interpreted as absolute estimates of migration requirements in units of distance per time. The metric's primary use, rather, is for relative comparisons among population and among species, assuming all other factors such as climatic tolerances and adaptive capacities are equal.

That said, from a management perspective, a relatively exact tracking of the climate niche of putative narrowly

adapted populations would be a conservative and cautious climate change adaptation strategy. Rather than relying on largely unknown climatic tolerances or adaptive capacities of populations, movement of planting stock according to the analogue velocity metrics used in this study in regular reforestation programs would minimise risks of maladaptation at little extra costs. When managing for optimal productivity rather than survival of populations, reasonably close tracking of the optimal climate niche of individual populations will be as important in future management as are current management strategies that match planting stock to their optimal current climate environments (Aitken and Whitlock 2013). Of course, any predictions of future climate environments from computer simulations contain their own assumptions and simplifications that may lead to large uncertainties, particularly for projections that approach the end of the 21st century as those used in this study (2080s). For practical conservation and management applications we therefore advocate a climatic analysis that relies on a shorter time horizon (e.g. 2020s) or on observed climate trends as exemplified by Gray et al. (2011).

In this study, we further restrict the search of climate analogues to within pairs of current and projected climate niche space, projected with species distribution models. Thus, we rely to some degree on the accuracy of palaeoclimatic reconstructions and the validity of assumptions inherent to models of the realised niche space of species (reviewed by Elith and Leathwick 2009, Svenning et al. 2011, Maguire et al. 2015). There is some reason to be doubtful about the accuracy of palaeoclimate simulations, given some of the apparent data-model mismatches in observed and modelled species ranges (Supplementary material Appendix 1). However, our analysis does not require the exact reconstruction of past or future species ranges. Rather, velocity calculations are largely independent of range predictions as they are carried out from any individual grid cell of a landscape to potential analogue climate grid cells in the past or future. A candidate cell outside the modelled climate niche is, by definition, not a close climate match to another cell within the niche. Geographic accuracy of predicted or reconstructed niche space does, however, factor into the analysis of overlapping species ranges to distinguish migration requirements that can be met through pollen flow (overlapping range portion), and those that require seed dispersal (non-overlapping) as shown in Fig. 3c.

The accuracy of habitat projections by means of species distribution models is also relevant for reverse velocities from projected future habitat to the current species range. They define the area where the species may be successfully managed in the future, whereas the velocity metric informs whether matching source populations are nearby or require human intervention in the form of assisted migration prescriptions. We propose that the modelled realised niche space, usually a severe limitation of species distribution models in assessing climate change vulnerabilities, should provide safe and conservative guidance as to where species should be maintained or introduced in the future. The rationale is that the realised climate niche is a subset of the total environmental tolerances of a species where it has demonstrated its ability to withstand biotic factors such as pest, diseases and competition.

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