# Conservation planning under climate change: accounting for adaptive potential and migration capacity in species distribution models

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## ABSTRACT

**Aim** A number of assumptions underpinning the use of species distribution models to predict biological responses to climate change are violated for temperate and boreal tree species that are widespread, long-lived and genetically adapted to local climate conditions. To address this situation, we propose a methodology to account for the potential effects of genetic structure, adaptive potential and limited migration capacity.

**Location** British Columbia, Canada.

**Methods** Similar to the widely used 'no migration' and 'unlimited migration' scenarios, we employ more refined biological response scenarios to evaluate the potential effects of genetic adaptation to local environments and the capacity of species to adapt and migrate. These scenarios are realized by two sets of geographic delineations that partition the species range into multiple populations and that subdivide the study area into smaller landscape units.

**Results** In a case study for British Columbia, we demonstrate how the approach can be used to evaluate the adequacy of a reserve system of 906 protected areas to ensure long-term maintenance of forest genetic resources for 48 tree species. We find that between 35% and 85% of locally adapted populations in protected areas are maintained under a median climate change scenario until the end of the century. A sensitivity analysis shows that assumptions about migration and adaptation capacity of species have a major effect on the projected conservation status.

**Main conclusions** We propose that the results of species distribution models have practical value for conservation planning if the focus is on maintenance rather than loss of suitable habitat. Accounting for genetic structure, adaptive potential and migration capacity through best-case and worst-case scenarios provide important information to effectively allocate limited resources available for conservation action.

**Keywords**
Bioclimate envelope models, climate change, conservation, genetic adaptation, migration, niche models.

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## INTRODUCTION

Species distribution models (SDMs) employ a variety of empirical, statistical or machine learning techniques to predict species occurrences from digital maps of predictor variables, such as interpolated climate data, topo-edaphic variables or other habitat factors (e.g. Guisan & Zimmer-

mann, 2000). Although there are exceptions (e.g. O'Neill *et al.*, 2008), SDMs normally predict the realized niche space of species. Predictive habitat maps have illustrated the discrepancy between current tree species distributions and their predicted potential habitat under climate change (e.g. Iverson & Prasad, 1998; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Loarie *et al.*, 2008). There has also been considerable

discussion of how tree populations might respond to the predicted habitat shifts through adaptation, migration or extirpation (Hamrick, 2004; Westfall & Millar, 2004; Aitken et al., 2008). Even for common tree species that are currently not at risk, the prospect of climate change has raised the question of how management intervention could minimize the loss of uniquely adapted tree populations (Ledig & Kitzmiller, 1992; Millar et al., 2007).

Species distribution models should be well suited to developing such climate-informed conservation strategies. In fact, the use of SDMs in conservation planning predates their application for habitat projections under climate change. They were first used to spatially extend species census data as the basis for reserve selection in the 1990s (Cabeza & Moilanen, 2001). The conceptual appeal is that species are more likely to persist or establish new populations in areas of suitable habitat. This suitable habitat can be better inferred from a statistical model parameterized with census data rather than directly from the census data themselves, as the latter often provide an incomplete snapshot of metapopulation distributions at one point in time. In addition, there is empirical evidence that local population extirpations because of metapopulation dynamics are negatively correlated with frequency, density or probability of occurrence inferred from SDMs (Araujo & Williams, 2000; Rodrigues et al., 2000; Araujo et al., 2002). In other words, species are more likely to persist in areas where models predict high frequencies or high probabilities of occurrence.

Using SDMs to inform conservation efforts under climate change is therefore a logical extension of their original purpose. Reserve selection, and evaluation of the effectiveness of existing reserves, under climate change has been carried out for birds and mammals (Araujo et al., 2004; Fuller et al., 2008; Hole et al., 2009) as well as for threatened plant species (Hannah et al., 2005, 2007; Rose & Burton, 2009). However, using SDMs to predict distributional shifts under climate change is problematic for temperate and boreal forest trees that are typically widespread, long-lived, genetically diverse and locally adapted. Habitat projections are probably too pessimistic in predicting habitat loss at the trailing edge of a species range, because SDMs are based on the realized niche, which, for trees, can be much narrower than the fundamental niche (Jackson & Overpeck, 2000). Also, the longevity, resilience and slow migration of tree populations make projections based on SDMs difficult to interpret (Hampe, 2004; Austin, 2007; Botkin et al., 2007). Projected loss of habitat does not necessarily imply an immediate problem for trees: once established, populations can persist a long time in non-native environments in the absence of major disturbance events, and if mortality does occur, local populations may have considerable potential to adapt to new environments (Hamrick, 2004; Westfall & Millar, 2004; Kuparinen et al., 2010). Further, it has been pointed out that geographic ranges of tree species have expanded and contracted repeatedly in response to glacial cycles in western North America, without many extinctions or significant losses of genetic diversity (Davis & Shaw, 2001; Botkin et al., 2007). Temporal and boreal tree species may therefore be less vulnerable to climate change than SDMs suggest.

Conversely, projections from SDMs are likely to be overly optimistic for the fate of northern and high-elevation populations under climate change. Here, suitable climate is generally predicted to be maintained at the species level. For example, the projected climate of a current Douglas-fir population in British Columbia by the 2080s may be closely equivalent to the climate of a current Douglas-fir population further south in Oregon. On this basis, a SDM will project that habitat is maintained for the British Columbia population throughout the 2080s, as conditions there remain within the realized niche of the species. However, if populations are genetically differentiated and locally adapted, climate change will have negative impacts not just at the trailing edge but throughout the species range, because all populations will occupy climates at or beyond the margins of their individual niches (Davis & Shaw, 2001; Hampe, 2004). There is now considerable evidence that genetic population structure should not be ignored when predicting distributional shifts under climate change for wide-ranging tree species. O'Neill et al. (2008) and Wang et al. (2006, 2010) predict reduced growth and survival of locally adapted lodgepole pine populations when genetic population structure is taken into account. In a range-wide dendrochronology study for Douglas-fir, Chen et al. (2010) show that northern and high-elevation populations are most vulnerable to climate change, while populations from the southern range limit appear relatively less affected because of adaptation to local climate conditions – a result opposite to projections from SDMs.

Ideally, modelling approaches are needed that include genetic, ecological and evolutionary processes (Botkin et al., 2007; Jeschke & Strayer, 2008; Thuiller et al., 2008). Such models, however, are not easy to develop, and their predictions are difficult to validate. In this study, we propose an alternative approach in which issues relating to genetic structure and resilience of populations are addressed through hypothetical biological response scenarios, rather than through direct modelling of demographic and evolutionary processes. In a case study for British Columbia, we illustrate how adaptation and migration may be integrated into SDMs in a simple way through best-case and worst-case scenarios of biological response to climate change. We further explore how to deal with uncertainties that arise from incomplete genetic and ecological information, differences between modelling methods, and other major factors that contribute to uncertainty in habitat projections.

## METHODS

### Scenarios of species response

One way to avoid direct modelling of demographic processes in SDMs is to make simple assumptions that represent best-case and worst-case scenarios. Such scenarios are useful for

conservation planning if the results indicate that there are threats even under the most optimistic scenario, or alternatively, that there is no major concern even under the most pessimistic scenario. For example, scenarios of *no migration* versus *unlimited migration* are widely used to interpret projections from SDMs (e.g. Peterson *et al.*, 2002; Araujo *et al.*, 2004; Thomas *et al.*, 2004). Here, we build a more comprehensive set of scenarios that account for genetic population structure, adaptive potential and migration capacity of tree species. These scenarios are realized by two sets of geographic delineations that partition the species range into multiple populations and that subdivide the study area into smaller landscape units. Hereafter, we refer to subdivisions of the species range as 'climatypes' following Tchebakova *et al.* (2009) in adopting Turesson's (1925) term for a conceptual population that exhibits a homogeneous adaptive profile to the environment in which it occurs. Secondly, we use the term 'landscape unit' for subdivisions of the study area. By allowing migration only within landscape units, we can implement more realistic migration scenarios. For example, we can evaluate SDM projections under the assumption that species can migrate to new habitat only within landscape units, such as small watersheds or protected areas.

For the case study in this study, we interpret maintenance of habitat for climatypes in protected areas as providing 'safe reserves' under climate change. It is therefore important that the delineation of climatypes should capture most of the adaptive genetic variation potentially occurring within a species. Erring on the side of delineating too many climatypes will result in a smaller number of identified 'safe reserves', but it does not compromise the inference that the reserves that we do find should contain suitable habitat under climate change projections. We approximate populations with a homogeneous adaptive profile in British Columbia using 14 biogeoclimatic zones (Meidinger & Pojar, 1991), which roughly correspond to seed zone delineations that reflect locally adapted genotypes (Hamann *et al.*, 2005). Transferring planting material within seed zones or biogeoclimatic zones would usually not be associated with significant reduction in growth and survival relative to local sources (Hamann *et al.*, 2005, 2011; Ying & Yanchuk, 2006). Approximately equivalent ecosystem classes that could be used elsewhere to delineate climatypes are the 'Ecoprovinces' of the National Ecological Framework for Canada (Selby & Santry, 1996), or the 'Level 3' delineation of the United States Ecoregion System (EPA, 2007). Another generic approach that could be used to approximate climatypes is the regionalization approach described by Mackey *et al.* (2008).

Secondly, we use protected area boundaries as landscape units to limit migration of tree species for the following case study. We only tally grid cells within a landscape unit as new habitat under future projections if the species was already present in the same landscape unit (in effect only allowing migration within a protected area). We, therefore, evaluate the protected area system independently from other managed forests and do not require that a matrix of surrounding forests is maintained to allow migration of new species and genotypes into protected areas under climate change.

These subdivisions of the study area and the species ranges allow the development of four biological scenarios that span a range of adaptation and migration possibilities for forest trees: (1) *no migration, no adaptation*, where species ranges are stratified into climatypes. Here, we only tally a grid cell as suitable habitat if the projections under current and future climate conditions have the same climatype in common; (2) *migration only* is similar to the first scenario, but new suitable habitat under a change in climate is only considered available if a climatype was previously present in the landscape unit (protected area in this case study); (3) *adaptation only,* where species ranges are not stratified into climatypes, and by implication, local populations are allowed to adapt to climate conditions that currently occur anywhere within the range of the species; and (4) *migration and adaptation*, which is a combination of scenario two and three, so that the only restriction to a species occupying suitable habitat within a landscape unit is that it must currently be present somewhere in that unit, implicitly only excluding long-distance dispersal events.

Compared with the standard *no migration* scenario, our scenario (1) *no migration no adaptation* will identify less habitat as maintained under climate change because it does not allow climate equivalents from the southern and low-elevation fringes of the species range to account for habitat maintenance at higher elevation and more northern locations, implying that the populations in those places are in no danger under climate change. Instead, the standard *no migration* scenario is equivalent to our (3) *adaptation only* scenario. Here, we allow populations to adapt to any conditions currently observed within the species range. This is also an implicit assumption of all SDMs that do not treat populations within a species separately. Compared with the standard *unlimited migration* scenario, our most optimistic scenario (4) *migration and adaptation* is more restrictive with respect to migration distances by not allowing migration beyond the boundaries of landscape units.

## Habitat projections for climatypes

To generate future habitat projections for climatypes, we build on an ecosystem-based modelling technique described in detail by Roberts & Hamann (2012). This approach predicts a dependent multi-level class variable (ecosystem classes used in this case as surrogates for climatypes) as a function of predictors that may include climate conditions, topographic indices and soil variables (in this study, we only use climate variables). Species distributions are subsequently derived by replacing the predicted ecosystem classes with known species frequencies for those classes that were estimated from forest inventory plots previously described by Hamann *et al.* (2005). For each species recorded in sample plots, we derived a percentage areal cover of the canopy projected to the ground, adjusted for the total canopy cover
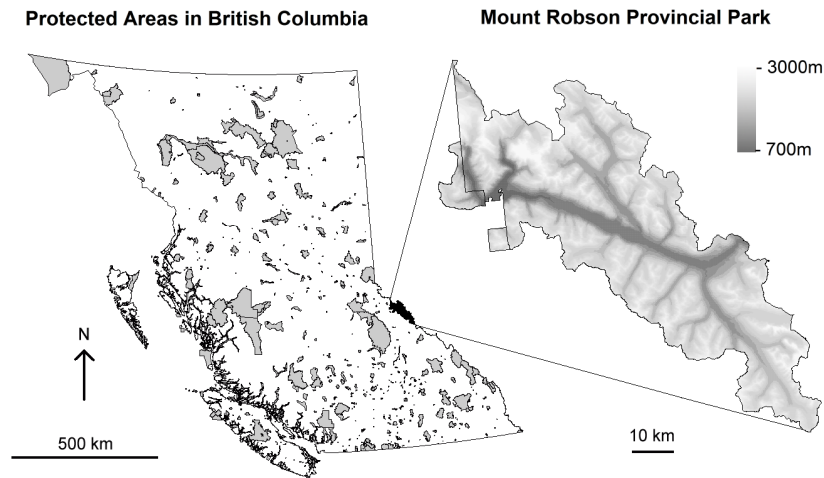
**Protected Areas in British Columbia**  **Mount Robson Provincial Park**



Figure 1 Protected area coverage of British Columbia and Mount Robson Provincial Park.

of the forest inventory plot. Species frequency for each eco-system unit was then calculated as the average percentage areal cover across all sample plots, including absence samples, that fall within an ecosystem polygon.

To allow an assessment of sensitivity, we use two different modelling approaches that can predict a nominal variable: discriminant analysis and the ensemble classifier RandomForests (for methodological details, see Hamann & Wang, 2006; Mbogga et al., 2010; Roberts & Hamann, 2012). The models predict several hundred fine-scale ecosystem classes, which we aggregate into broader climatypes that represent locally adapted populations of wide-ranging tree species (described later with a detailed example).

As predictor variables, we used mean annual temperature, mean warmest month temperature, mean coldest month temperature, continentality (difference between mean January and mean July temperature), mean annual precipitation, mean growing season precipitation (May–September), annual heat moisture index, summer heat moisture index, number of forest free days, chilling degree days below 0°C, growing degree days above 5°C and extreme minimum temperature. Topographic and edaphic variables were not included because, based on available data, these variables have proved to be poor predictors in the complex landscapes of British Columbia (Mbogga et al., 2010). Grids for climate variables were generated through interpolation of weather station data using the Parameter Regression of Independent Slopes (PRISM) methodology (Daly et al., 2008). Subsequently, biologically relevant climate variables were generated at 400 m resolution using the ClimateBC software package that is freely available[1] (Hamann & Wang, 2005; Wang et al., 2006; Mbogga et al., 2009). The high resolution was primarily chosen to accurately represent temperature gradients in mountainous areas of British Columbia.

[1]Available for download at http://www.genetics.forestry.ubc.ca/cfcg/climate-models.html

For an evaluation of 48 species in 906 protected areas, we use a median climate change scenario for British Columbia, the Canadian model CGCM2, emission scenario B1 (Mbogga et al., 2009). However, to provide an example of how uncertainty in model projections may be dealt with in conservation planning, we also predict suitable habitat for western red cedar (Thuja plicata) in a single large protected area, Mount Robson Provincial Park, using climate change projections for four major SRES emission and population growth scenario families (A1FI, A2, B1, B2) and implementations of these scenarios by five modelling groups (CGCM2, Canada; HADCM3, UK; ECHAM4, Europe; CSIRO2, Australia; and PCM, United States). For this case study, climate change projections for the 2050s were added as deviations from the 1961–90 normal period to the high-resolution baseline climate dataset. We further use the difference between the 1961–90 climate normal and the 1997–2006 decadal average to represent climate trends observed over an approximately 25-year period (mid-point of normal period to mid-point of decadal average). This anomaly surface was used for predictive habitat modelling in the same way as projections from general circulation models (Mbogga et al., 2009).

**Protected area evaluations**

The conservation status of locally adapted tree populations was carried out using a standard gap analysis approach, previously implemented for forest inventory and sample plot data (Hamann et al., 2004, 2005; Chourmouzis et al., 2009). Here we extend this approach to evaluate projected habitat under current and expected future climate conditions. We evaluated habitat projections for permanent protected areas that exclude all resource extraction, which includes national parks, ecological reserves, recreation areas, and class A and C provincial parks of British Columbia (Fig. 1). Protected areas were tallied as containing sufficient habitat for a species if the current or projected aerial cumulative cover of a species exceeds 10 ha, which approximately corresponds to a census

size of 5000, and an effective population size of at least 1000 mature-equivalent individuals (Hamann et al., 2004, 2005; Chourmouzis *et al.*, 2009). For example, if a species is predicted to have 200 ha of suitable habitat within a protected area and an average species frequency of 5%, the threshold requirement of 10 ha cumulative cover would be exactly satisfied. The implied effective population size of 1000 mature individuals is generally considered sufficient for the long-term operation of evolutionary processes, balancing losses of alleles because of genetic drift and gains of alleles because of mutation, and maintaining genetic diversity including relatively rare alleles (Aitken, 2000; Yanchuk, 2001).

## RESULTS

### Habitat projections for climatypes and species

In the following example for a single protected area, we illustrate how the four migration and adaptation scenarios were

implemented. Predicted ecosystem variants were reclassified into macroclimatic zones to infer climatypes, which were subsequently used to structure species distributions (Fig. 2). Projected species distributions were obtained by substituting expected species frequencies for each ecosystem variant (Fig. 3). To arrive at the amount of available habitat in a protected area, we then counted the grid cells assigned to each climatype within the species distribution (e.g. in Figs 2 and 3, the climatype of western red cedar supported in the reserve is almost exclusively Interior Cedar Hemlock (ICH) for all time periods).

In this example, Mt Robson Provincial Park supports a large enough population size for the ICH climatype at present because the population size inferred from inventory data and the modelled habitat (Fig. 3, mapped and modelled) is above our threshold value of 10 ha cumulative cover. The reserve is further considered suitable for the 2020s, 2050s and 2080s under the biological scenarios (1) *no migration, no adaptation* and (3) *adaptation only* as there is no
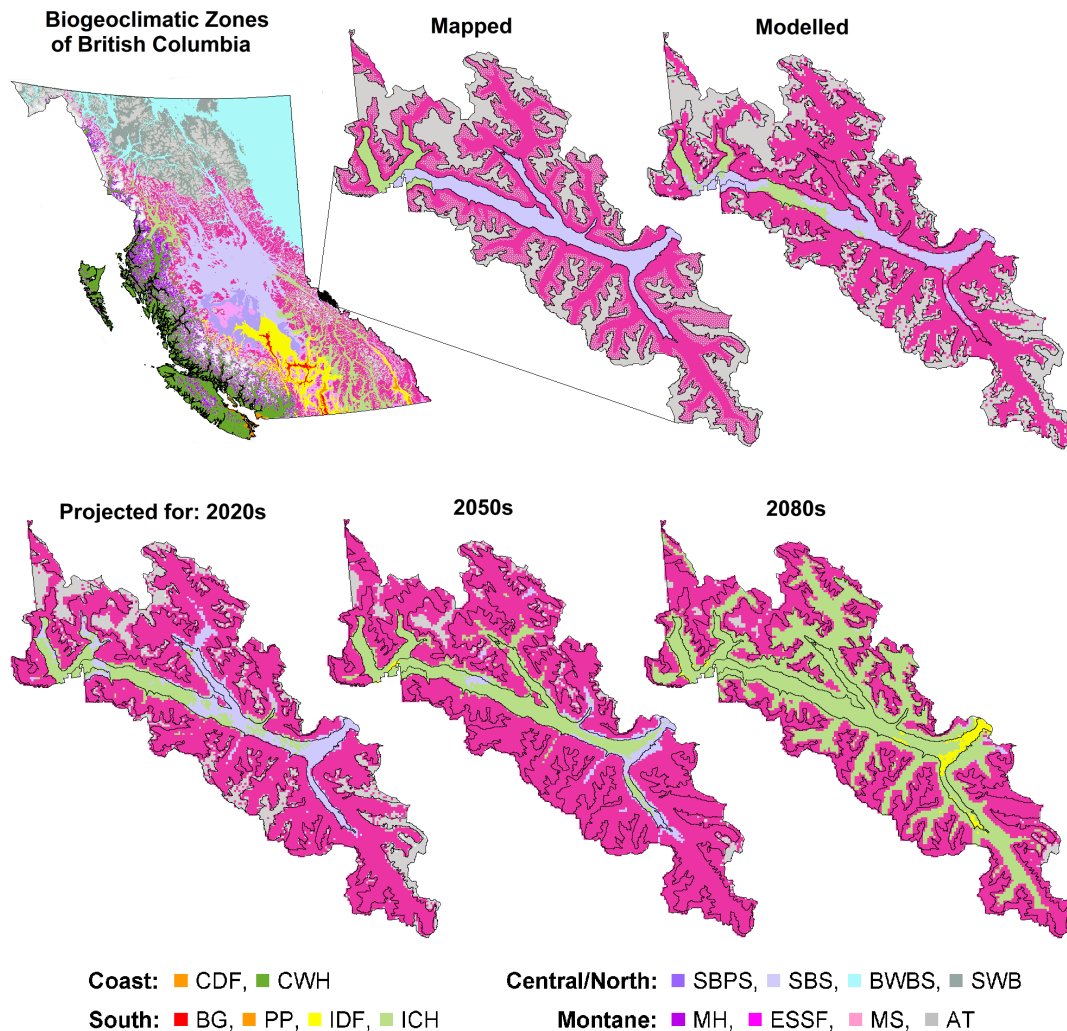


Biogeoclimatic Zones of British Columbia

Mapped

Modelled

Projected for: 2020s

2050s

2080s

**Coast:** ■ CDF, ■ CWH    **Central/North:** ■ SBPS, ■ SBS, ■ BWBS, ■ SWB

**South:** ■ BG, ■ PP, ■ IDF, ■ ICH    **Montane:** ■ MH, ■ ESSF, ■ MS, ■ AT

**Figure 2** Mapped and predicted ecosystem climate envelopes, summarized at the zone level of biogeoclimatic ecological classification system for Mt Robson Provincial Park based on climate change predictions of CGCM2-B1 (names of zones for the park area: IDF, interior Douglas-fir; IDH, Interior Cedar Hemlock; SBS, sub-boreal spruce; ESSF, Engelmann spruce-subalpine fir; AT, Alpine tundra)
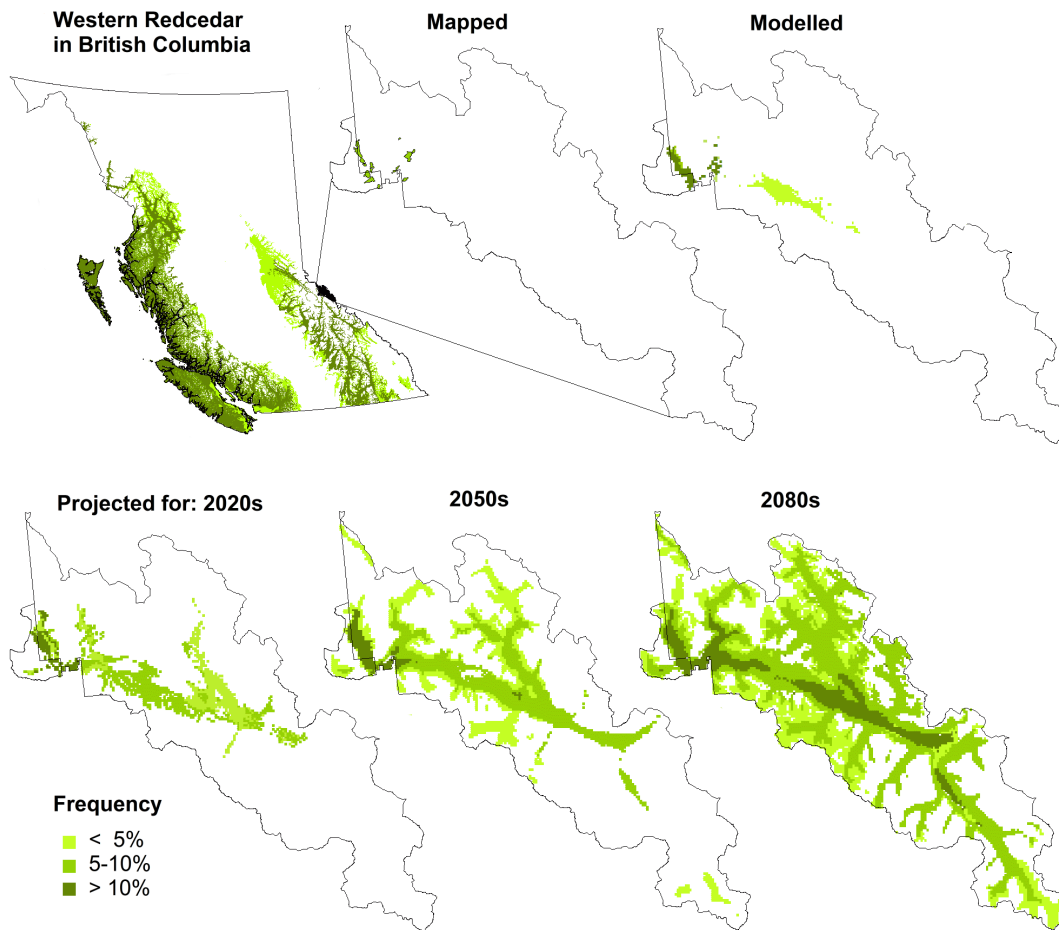
**Figure 3** Observed and predicted species frequencies for western red cedar (*Thuja plicata*) for Mt Robson Provincial Park based on climate change predictions of CGCM2-B1.

appreciable loss of current ICH-type habitat. For the scenarios that allow migration to new habitat within the reserve, the amount of suitable habitat for the ICH climatype of western red cedar expands considerably. To appreciate the difference between the biological scenarios (2) *migration only* and (4) *migration and adaptation*, consider the emergence of the interior Douglas-fir (IDF) climatype in the 2080s (Fig. 2, yellow). This habitat patch is outside the current species distribution, so it would require migration to new habitat within the reserve, but it also represents a climatype that was not previously present in the reserve, and therefore, western red cedar populations of the ICH climatype would need to adapt to IDF-type climate conditions. The reserve would consequently only be considered to support a population of the IDF climatype by the 2080s under our most optimistic biological scenario (4) *migration and adaptation*.

## Conservation status of 48 tree species under climate change

The same evaluation was carried out for the climatypes of all 48 tree species in all 906 protected areas of British Columbia (Table 1, further summarized in Fig. 4). Predictions for the

persistence of adequate habitat varied considerably among species as well as among adaptation and migration scenarios. The *migration and adaptation* scenario predicted the maintenance of approximately 85% of populations in protected areas that meet the minimum population size threshold by the 2080s (Fig. 4). This includes an improvement of overall conservation status for the 2020s because of habitat projections exceeding the 10 ha threshold requirement in cases where it is currently not met. Also under the *adaptation only* scenario, a considerable proportion of populations would continue to find suitable habitat in protected areas. The *migration only* scenario predicted maintenance of approximately half of the protected populations by the 2080s, while the most pessimistic *no adaptation, no migration* scenario, still predicted maintenance of 35% of the locally adapted populations in protected areas by the 2080s.

The projected conservation status of species depends to a large extent on their distribution in British Columbia relative to their global range. Species that currently have their southern range limits in British Columbia are predicted to lose suitable habitat in reserves regardless of biological scenarios (e.g. *Larix laricina*, *Picea glauca* and *P. mariana*). For these species, having sufficient genetic diversity to adapt to new
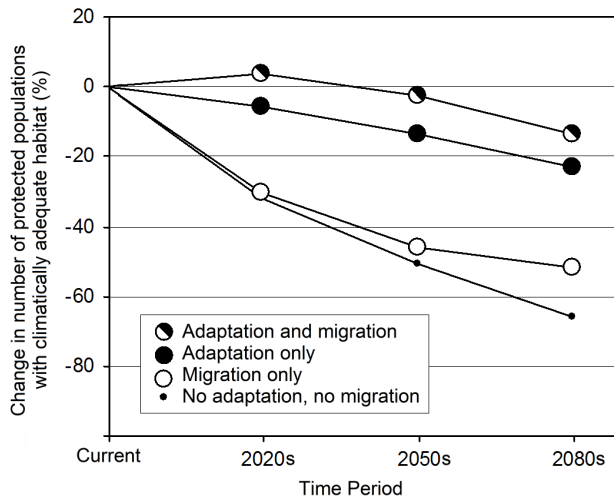
Figure 4 Change in the number of adequately protected climatypes of 48 tree species in 906 protected areas of British Columbia. The figure summarizes data contained in Table 1 evaluating habitat projections under a median (CGCM2-B1) climate change scenario and four biological response scenarios.

climate conditions is generally more important than the capacity to migrate, which is reflected in the high numbers under the *adaptation only* scenario relative to the *no adaptation, no migration* scenario (Table 1). Species that have populations further south in the United States, but their range centre and their highest frequencies located further north in Canada, are also predicted to lose most habitat under the *no migration* scenario (e.g. *Abies lasiocarpa*, *Betula papyrifera*, *Populus tremuloides* and *P. balsamifera*).

For species occurring in mountainous areas, where suitable habitat shifts primarily along elevational gradients, both the capacity for adaptation and the ability to migrate within a protected area to new potential habitat have a positive effect on the total number of protected areas with suitable habitat (e.g. *Alnus tenuifolia*, *Abies lasiocarpa*, *Tsuga mertensiana*). Species that currently have their northern range limits in British Columbia generally maintain their conservation status at least under the two biological scenarios that allow adaptation. For this group of species, the count of suitable protected areas increases significantly if the migration to new habitat within a reserve is allowed (e.g. *Abies grandis*, *Acer circinatum* and *A. macrophyllum* for the coast, as well as *Prunus emarginata*, *Pinus monticola* and *P. ponderosa* for the interior of British Columbia). For species with high-elevation and northern range limits within the study area, the capacity to migrate almost always has a larger positive effect than the capacity to adapt within a protected area status under climate change. This is reflected in the high numbers under the *migration only* scenario relative to the *no adaptation, no migration* scenario (Table 1).

Finally, montane species that only occur at very high elevation are projected to lose suitable habitat in protected areas regardless of the biological scenario (i.e. *Larix lyallii*,

*Pinus albicaulis*), and the least change in the overall conservation status, also regardless of biological scenario, was projected for species with coastal or interior wet forest distributions in British Columbia (e.g. *Alnus rubra*, *Picea sitchensis*, *Tsuga heterophylla*, *Thuja plicata*). Only species that occur at higher elevation in these wet ecosystems experience a moderate decline in the number of populations maintained under suitable climate conditions (e.g. *Chamaecyparis nootkatensis*, *Tsuga mertensiana*).

Under our *no migration, no adaptation* scenario, a much smaller number of populations are maintained in protected areas than under the standard *no migration* scenario of other studies, which is here represented as *adaptation only* (Fig. 4). Also, our constrained migration scenario appears decidedly conservative, although we did not include the corresponding *unlimited migration* scenario of other studies for a direct comparison. The latter often allows migration over hundreds or thousands of kilometres. Allowing migration just within protected areas in British Columbia results in only a small benefit relative to the *no migration, no adaptation* scenario (Fig. 4).

### Sensitivity analysis for Mt. Robson Provincial Park

The major differences among our biological response scenarios in projected conservation status illustrate the conservation challenges that climate change may bring. However, the differences presented to this point do not reflect other sources of uncertainty in climate change or modelling methods that will add more uncertainty to forecasts (Dormann, 2007; Sinclair *et al.*, 2010). While a comprehensive sensitivity analysis for all species in all protected areas is beyond the scope of this study, we illustrate a possible approach to deal with uncertainty because of multiple factors for western red cedar (*Thuja plicata*) in Mount Robson Provincial Park (Figs 2 and 3). In this case, the predicted effects of migration and adaptation scenarios at this landscape scale were much larger, often by an order of magnitude, than the effects of using different general circulation models, emission scenarios or modelling methods (Table 2).

From an applied conservation perspective, the key result from this analysis is that under almost all combinations of biological response scenarios, climate models, emission scenarios and modelling methods, the Mt. Robson Provincial Park is predicted to maintain sufficient habitat for western red cedar populations, and in particular, the Interior Cedar Hemlock (ICH) climatype. We would therefore regard this protected area as a safe reserve for the ICH climatype of the species, and it could enter as a positive count into a revised Table 1, which is currently based on just one scenario with one predictive method. To generalize the approach, we would need to decide on the proportion of positive projections above which we would regard a reserve as safe (e.g. 90% of projections for each biological scenario).

Table 1 Number of protected areas that maintain a sufficient amount of suitable habitat (area × expected species frequency ≥ 10 ha) under four adaptation and migration scenarios. The climate change scenario used for this analysis is CGCM2-B1, an approximately median climate change scenario for BC with respect to mean annual temperature and precipitation.

| Species | Current | No Adapt., No Migr. | | | Migration only | | | Adaptation only | | | Adapt. and Migr. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2020s | 2050s | 2080s | 2020s | 2050s | 2080s | 2020s | 2050s | 2080s | 2020s | 2050s | 2080s |
| *Abies amabilis* | 149 | 129 | 113 | 80 | 152 | 136 | 98 | 131 | 117 | 96 | 154 | 143 | 109 |
| *Abies grandis* | 20 | 21 | 21 | 13 | 32 | 51 | 75 | 23 | 26 | 25 | 34 | 55 | 87 |
| *Abies lasiocarpa* | 295 | 187 | 103 | 65 | 199 | 133 | 83 | 260 | 217 | 171 | 266 | 233 | 181 |
| *Acer circinatum* | 55 | 47 | 51 | 54 | 64 | 75 | 85 | 47 | 51 | 55 | 65 | 76 | 89 |
| *Acer glabrum* | 102 | 95 | 74 | 73 | 119 | 104 | 101 | 112 | 123 | 126 | 132 | 143 | 149 |
| *Acer macrophyllum* | 55 | 65 | 67 | 64 | 76 | 86 | 93 | 74 | 81 | 95 | 86 | 101 | 125 |
| *Alnus tenuifolia* | 164 | 86 | 37 | 21 | 115 | 67 | 53 | 153 | 140 | 107 | 175 | 159 | 126 |
| *Alnus rubra* | 126 | 129 | 127 | 127 | 133 | 137 | 133 | 137 | 146 | 164 | 142 | 157 | 172 |
| *Alnus viridis* | 253 | 146 | 70 | 32 | 165 | 107 | 76 | 234 | 195 | 145 | 244 | 206 | 159 |
| *Arbutus menziesii* | 2 | 1 | 1 | 1 | 2 | 4 | 5 | 3 | 4 | 5 | 3 | 7 | 11 |
| *Betula occidentalis* | 16 | 10 | 7 | 3 | 22 | 28 | 28 | 14 | 17 | 7 | 26 | 38 | 34 |
| *Betula papyrifera* | 154 | 127 | 97 | 94 | 140 | 124 | 130 | 180 | 192 | 190 | 191 | 209 | 216 |
| *Chamaec. nootkatensis* | 111 | 96 | 75 | 40 | 109 | 91 | 55 | 101 | 83 | 53 | 113 | 97 | 63 |
| *Cornus nuttallii* | 14 | 12 | 12 | 11 | 22 | 31 | 33 | 15 | 19 | 25 | 24 | 37 | 46 |
| *Corylus cornuta* | 35 | 37 | 28 | 28 | 64 | 63 | 65 | 39 | 39 | 40 | 67 | 70 | 74 |
| *Juniperus scopulorum* | 15 | 8 | 8 | 2 | 13 | 12 | 10 | 10 | 11 | 5 | 17 | 16 | 16 |
| *Larix laricina* | 33 | 0 | 0 | 0 | 8 | 10 | 9 | 33 | 23 | 6 | 36 | 30 | 17 |
| *Larix lyallii* | 21 | 4 | 0 | 0 | 6 | 1 | 0 | 4 | 0 | 0 | 7 | 1 | 0 |
| *Larix occidentalis* | 39 | 18 | 11 | 0 | 44 | 55 | 53 | 29 | 33 | 26 | 51 | 70 | 66 |
| *Malus fusca* | 39 | 43 | 36 | 30 | 47 | 40 | 39 | 43 | 41 | 39 | 47 | 45 | 48 |
| *Picea engelmannii* | 191 | 97 | 76 | 46 | 127 | 104 | 74 | 166 | 165 | 135 | 181 | 177 | 149 |
| *Picea glauca* | 169 | 69 | 13 | 5 | 85 | 35 | 17 | 142 | 101 | 61 | 150 | 111 | 67 |
| *Picea mariana* | 138 | 43 | 7 | 1 | 59 | 30 | 16 | 117 | 90 | 57 | 129 | 100 | 65 |
| *Picea sitchensis* | 134 | 125 | 105 | 85 | 129 | 117 | 94 | 128 | 113 | 94 | 134 | 123 | 101 |
| *Pinus albicaulis* | 87 | 40 | 16 | 4 | 61 | 38 | 22 | 50 | 30 | 8 | 67 | 47 | 25 |
| *Pinus contorta* | 375 | 247 | 162 | 116 | 263 | 201 | 158 | 354 | 311 | 263 | 361 | 331 | 280 |
| *Pinus monticola* | 54 | 52 | 50 | 40 | 75 | 88 | 82 | 58 | 64 | 60 | 80 | 100 | 98 |
| *Pinus ponderosa* | 59 | 46 | 36 | 20 | 60 | 66 | 62 | 77 | 90 | 116 | 89 | 113 | 144 |
| *Populus balsamifera* | 212 | 126 | 88 | 82 | 151 | 128 | 125 | 205 | 206 | 218 | 219 | 230 | 250 |
| *Populus tremuloides* | 205 | 107 | 53 | 31 | 122 | 78 | 61 | 198 | 185 | 161 | 204 | 193 | 176 |
| *Prunus emarginata* | 4 | 5 | 9 | 12 | 10 | 20 | 39 | 5 | 9 | 13 | 10 | 20 | 41 |
| *Prunus pensylvanica* | 7 | 5 | 2 | 0 | 9 | 4 | 0 | 5 | 2 | 0 | 9 | 4 | 0 |
| *Prunus virginiana* | 19 | 9 | 6 | 7 | 16 | 14 | 26 | 17 | 27 | 42 | 24 | 37 | 58 |
| *Pseudotsuga menziesii* | 385 | 342 | 295 | 263 | 379 | 330 | 296 | 412 | 421 | 413 | 450 | 455 | 439 |
| *Quercus garryana* | 10 | 9 | 9 | 9 | 10 | 10 | 10 | 9 | 9 | 9 | 10 | 10 | 10 |
| *Rhamnus purshiana* | 5 | 6 | 8 | 8 | 13 | 20 | 24 | 6 | 11 | 15 | 13 | 23 | 31 |
| *Salix bebbiana* | 72 | 27 | 6 | 8 | 40 | 21 | 20 | 56 | 53 | 44 | 70 | 63 | 56 |
| *Salix discolor* | 7 | 0 | 0 | 0 | 5 | 3 | 1 | 5 | 1 | 0 | 9 | 4 | 1 |
| *Salix lucida* | 43 | 17 | 12 | 12 | 30 | 29 | 28 | 26 | 14 | 20 | 40 | 30 | 35 |
| *Salix scouleriana* | 93 | 37 | 11 | 6 | 54 | 37 | 29 | 80 | 76 | 48 | 90 | 88 | 67 |
| *Salix sitchensis* | 92 | 65 | 48 | 46 | 87 | 79 | 74 | 80 | 63 | 62 | 102 | 90 | 85 |
| *Taxus brevifolia* | 76 | 72 | 70 | 55 | 93 | 102 | 93 | 74 | 76 | 64 | 96 | 109 | 105 |
| *Thuja plicata* | 344 | 300 | 277 | 246 | 320 | 297 | 260 | 351 | 346 | 333 | 364 | 363 | 349 |
| *Tsuga heterophylla* | 345 | 302 | 280 | 241 | 313 | 288 | 253 | 317 | 303 | 285 | 328 | 315 | 296 |
| *Tsuga mertensiana* | 138 | 110 | 67 | 34 | 122 | 87 | 60 | 115 | 87 | 56 | 128 | 103 | 72 |

We should also be conscious that, ultimately, climate-informed natural resource management and conservation has to be guided by climate trends as they materialize at fine scales and impact tree populations locally. We, therefore, find it useful to include observed climate change as input data for model projections (Table 2, last row). Interestingly, these model runs show some of the lowest habitat values for western red cedar in Mt Robson Provincial Park, primarily because of a regional reduction in precipitation over the last 25 years that exceeds all climate change projections (Mbogga *et al.*, 2009).

**Table 2** Maintenance of suitable habitat for western red cedar (*Thuja plicata*) in the Mt Robson Provincial Park. The amount of suitable habitat is given as cumulative cover (area × expected species frequency) in units of hectare, and the projections are for different combinations of climate change predictions for the 2050s, modelling methods (DA, discriminant analysis; RF, RandomForest), and biological response scenarios. The cumulative cover modelled under the 1961–90 baseline climate is 391 ha. The median climate change scenario used to derive Table 1 is highlighted in bold.

| GCM/Scenario | Migration only | | Adaptation only | | Adapt. and Migr. | | No Adapt., No Migr. | |
|---|---|---|---|---|---|---|---|---|
| | DA | RF | DA | RF | DA | RF | DA | RF |
| CGCM/A1FI | 1115 | 3250 | 170 | 373 | 1213 | 3967 | 158 | 371 |
| CGCM/A2 | 1371 | 1779 | 231 | 334 | 1392 | 1804 | 228 | 332 |
| **CGCM/B1** | **1967** | **2390** | **251** | **278** | **3144** | **2529** | **245** | **264** |
| CGCM/B2 | 2206 | 1559 | 270 | 336 | 2226 | 1697 | 263 | 327 |
| CSIRO/A1FI | 3402 | 3802 | 222 | 372 | 3785 | 5378 | 210 | 367 |
| CSIRO/A2 | 1529 | 4081 | 253 | 378 | 1583 | 5707 | 233 | 376 |
| CSIRO/B1 | 641 | 3089 | 30 | 371 | 660 | 3835 | 0 | 370 |
| CSIRO/B2 | 4190 | 4594 | 117 | 378 | 5483 | 7584 | 64 | 376 |
| ECHAM/A2 | 589 | 508 | 137 | 159 | 599 | 511 | 134 | 147 |
| ECHAM/B2 | 1056 | 2473 | 131 | 189 | 1096 | 2576 | 123 | 166 |
| HADCM/A1FI | 1482 | 6579 | 249 | 322 | 1594 | 6984 | 245 | 313 |
| HADCM/A2 | 729 | 5982 | 140 | 244 | 739 | 6059 | 134 | 220 |
| HADCM/B1 | 1050 | 2077 | 92 | 219 | 1115 | 2225 | 47 | 191 |
| HADCM/B2 | 1179 | 5552 | 217 | 199 | 1288 | 6192 | 204 | 171 |
| PCM/A1FI | 1027 | 1300 | 258 | 308 | 1089 | 1411 | 239 | 303 |
| PCM/A2 | 764 | 978 | 223 | 256 | 793 | 1088 | 198 | 244 |
| PCM/B1 | 514 | 5645 | 145 | 226 | 529 | 5876 | 128 | 215 |
| PCM/B2 | 677 | 1193 | 146 | 259 | 715 | 1295 | 134 | 239 |
| 25-year Trend | 1214 | 777 | 106 | 117 | 1296 | 794 | 88 | 103 |

## DISCUSSION

### Implications for conservation planning

Habitat projections from SDMs are widely recognized as an imperfect approach to infer population dynamics in response to climate change. Limitations and research challenges have been thoroughly discussed elsewhere (e.g. Pearson & Dawson, 2003; Hampe, 2004; Guisan *et al.*, 2006; Austin, 2007; Botkin *et al.*, 2007; Dormann, 2007; Thuiller *et al.*, 2008) and recently reviewed in the context of conservation planning (Sinclair *et al.*, 2010). The general consensus is that inferences that seem most important to conservation planning often cannot be made reliably. For example, a projected loss of habitat does not necessarily mean a population will be threatened for various reasons: SDMs do not model the broader fundamental niche space that describes the abiotic tolerances of species; other species may be impacted equally or more by climate change, resulting in reduced competition; or species may survive in favourable microsites at scales not addressed by SDMs.

We feel, however, that one inference from species distribution modelling remains broadly valid, and this inference can make an important contribution to conservation planning if carefully interpreted. Habitat projected to be maintained in areas where the species already exists today can generally be interpreted as constituting a 'safe reserve'. This inference does not appear to violate model assumptions: that is, the species remains within its realized niche space; new biotic interactions may arise under climate change, but the species has also managed to survive under comparable conditions elsewhere in its current range; and scale issues would be improbable as the species finds suitable microsites under comparable conditions elsewhere in its current range.

Our study strengthens this inference for temperate and boreal tree species. The existence of genetic structure and locally adapted populations is problematic in this case, because climate change will have negative impacts not just at the trailing edge where habitat is usually lost, but throughout the species range because all populations will occupy climates at or beyond the margins of their individual niches (Davis & Shaw, 2001; Hampe, 2004; Chen *et al.*, 2010). Analysing maintenance of suitable habitat for tree species' climatypes, here defined as approximations of populations with homogenous adaptive profiles, solves this problem by means of a straightforward extension to existing species distribution modelling techniques.

The inference of areas likely to maintain suitable habitat for tree species' climatypes has important practical applications. Projections, for example, could inform expensive habitat restoration efforts by confirming that suitable climate habitat will probably be maintained for target species under most climate change scenarios. Conversely, we can avoid 'uphill battles' where we may inadvertently try to conserve

populations in areas that no longer contain suitable climate conditions. Maintenance of suitable habitat at the climatype level also provides the necessary information for practitioners to guide reforestation programmes or assisted migration efforts. Establishment of species through planting always requires the selection of suitably adapted planting stock in addition to decisions about which species should be the target of conservation efforts (Marris, 2009; McKenney *et al.*, 2009; Gray & Hamann, 2011; Gray *et al.*, 2011).

## Dealing with uncertainty and unknown biological parameters

We have proposed refinements to the widely used best-case and worst-case scenarios, such as *no migration* versus *unlimited migration*, to account for genetic population structure and adaptive potential of tree species. Such scenarios are useful for conservation planning if the results indicate that there are threats even under the most optimistic scenario, or alternatively, that there is no major concern even under the most pessimistic scenario. Technically, the implementation of our proposed biological response scenarios requires only the subdivision of the species into climatypes for *adaptation* scenarios and the subdivision of the landscape into appropriate units for *migration* scenarios (e.g. ranging in size from small catchment areas to large watersheds). In principle, using landscape subdivisions as a substitute for complex spatial processes is not a new idea. For example, Klein *et al.* (2009) used the same approach to incorporate ecological and evolutionary processes into continental-scale conservation planning. Botkin *et al.* (2007) suggested that separate models could be developed for different climatypes if there are sufficient census data.

As these subdivisions determine the outcome of modelling, they have to be chosen carefully. We find it a useful to ask: are there any 'safe reserves' left for a species or locally adapted population if we make multiple worst-case assumptions, for example, no migration capacity, no adaptation capacity, strong genetic structure (represented by many climatypes), and a requirement of enough maintained habitat to support an effective population size that can maintain evolutionary processes in isolation. For individual species, where we do have ecological or genetic data, these assumptions could be relaxed. The *no migration* scenarios might be a reasonable approximation for species with low fecundity and lack of long-distance dispersal (e.g. *Quercus garryana*, *Corylus cornuta*), but for species that have early maturation, high fecundity and high vagility (e.g. *Alnus*, *Betula*, *Salix*, *Populus*), our *migration* scenarios may be more realistic. While, for tree species with low levels of within-population genetic diversity, e.g. *Cornus nuttallii* (Keir et al. 2011), the no adaptation scenarios will usually be appropriate, the *adaptation* scenario may be realistic for either very high levels of within-population genetic variation or if there is little genetic population structure and high phenotypic plasticity

as for example in western red cedar (Rehfeldt, 1994). In such cases, a species can be treated as a homogenous unit, which is in fact equivalent to the *adaptation only* scenario.

This focus on maintenance of suitable habitat further allows us to incorporate uncertainty in model projections in a straightforward way. The consensus approach proposed by Araujo & New (2007) based on a variety of predictive methods and climate change scenarios could be implemented as demonstrated in principle for the Mt. Robson Provincial Park case study. A more comprehensive analysis could also analyse multiple sources of uncertainty, similar to Mbogga *et al.* (2010), and require that habitat must be maintained in a protected area under a sufficient number of model runs (e. g. 90%) to be counted as a safe reserve for a species or locally adapted population.

## REFERENCES

Aitken, S.N. (2000) Conserving adaptive variation in forest ecosystems. *Journal of Sustainable Forestry*, **10**, 1–12.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T.L. & Curtis-Mclane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.

Araujo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22**, 42–47.

Araujo, M.B. & Williams, P.H. (2000) Selecting areas for species persistence using occurrence data. *Biological Conservation*, **96**, 331–345.

Araujo, M.B., Williams, P.H. & Fuller, R.J. (2002) Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society B*, **269**, 1971–1980.

Araujo, M.B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, **10**, 1618–1626.

Austin, M. (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling*, **200**, 1–19.

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.

Cabeza, M. & Moilanen, A. (2001) Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution*, **16**, 242–248.

Chen, P., Welsh, C. & Hamann, A. (2010) Geographic variation in growth response of Douglas-fir to inter-annual climate variability and projected climate change. *Global Change Biology*, **16**, 3374–3385.

Chourmouzis, C., Yanchuk, A.D., Hamann, A., Smets, P. & Aitken, S.N. (2009). Forest tree genetic conservation status report 1: In situ conservation status of all indigenous British Columbia species. B.C. Min. For. Range, Victoria, B.C. Tech. Rep. 53. ISBN: 978-0-7726-6181-4.

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J. & Pasteris, P.P. (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, **28**, 2031–2064.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.

Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, **8**, 387–397.

EPA (2007) Ecoregion Maps and GIS Resources. U.S. Environmental Protection Agency, Corvallis, OR, Western Ecology Division official website, Available at: http://www.epa.gov/wed (accessed 10 May 2008).

Fuller, T., Morton, D.P. & Sarkar, S. (2008) Incorporating uncertainty about species' potential distributions under climate change into the selection of conservation areas with a case study from the Arctic Coastal Plain of Alaska. *Biological Conservation*, **141**, 1547–1559.

Gray, L.K. & Hamann, A. (2011) Strategies for reforestation under uncertain future climates: guidelines for Alberta, Canada. *PLoS ONE*, **6**, e22977.

Gray, L.K., Gylander, T., Mbogga, M.S., Chen, P.Y. & Hamann, A. (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecological Applications*, **21**, 1591–1603.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J.M.C., Aspinall, R. & Hastie, T. (2006) Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology*, **43**, 386–392.

Hamann, A. & Wang, T.L. (2005) Models of climatic normals for genecology and climate change studies in British Columbia. *Agricultural and Forest Meteorology*, **128**, 211–221.

Hamann, A. & Wang, T.L. (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, **87**, 2773–2786.

Hamann, A., Aitken, S.N. & Yanchuk, A.D. (2004) Cataloguing in situ protection of genetic resources for major commercial forest trees in British Columbia. *Forest Ecology and Management*, **197**, 295–305.

Hamann, A., Smets, P., Yanchuk, A.D. & Aitken, S.N. (2005) An ecogeographic framework for in situ conservation of forest trees in British Columbia. *Canadian Journal of Forest Research*, **35**, 2553–2561.

Hamann, A., Gylander, T. & Chen, P. (2011) Developing seed zones and transfer guidelines with multivariate regression trees. *Tree Genetics and Genomes*, **7**, 399–408.

Hampe, A. (2004) Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, **13**, 469–471.

Hamrick, J.L. (2004) Response of forest trees to global environmental changes. *Forest Ecology and Management*, **197**, 323–335.

Hannah, L., Midgley, G., Hughes, G. & Bomhard, B. (2005) The view from the cape. Extinction risk, protected areas, and climate change. *BioScience*, **55**, 231–242.

Hannah, L., Midgley, G., Andelman, S., Araujo, M., Hughes, G., Martinez-Meyer, E., Pearson, R. & Williams, P. (2007) Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, **5**, 131–138.

Hole, D.G., Willis, S.G., Pain, D.J., Fishpool, L.D., Butchart, S.H.M., Collingham, Y.C., Rahbek, C. & Huntley, B. (2009) Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters*, **12**, 420–431.

Iverson, L.R. & Prasad, A.M. (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*, **68**, 465–485.

Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.

Jeschke, J.M. & Strayer, D.L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. Year in Ecology and Conservation Biology 2008. *Annals of the New York Academy of Sciences*, **1134**, 1–24.

Keir, K.R., Bemmels, J.B. & Aitken, S,N. (2011) Low genetic diversity, moderate local adaptation, and phylogeographic insights in Cornus nuttallii (Cornaceae). *American Journal of Botany*, **98**, 1327–1336.

Klein, C., Wilson, K., Watts, M., Stein, J., Berry, S., Carwardine, J., Smith, M.S., Mackey, B. & Possingham, H. (2009) Incorporating ecological and evolutionary processes into continental-scale conservation planning. *Ecological Applications*, **19**, 206–217.

Kuparinen, A., Savolainan, O. & Schurr, F.M. (2010) Increased mortality can promote evolutionary adaptation of forest trees to climate change. *Forest Ecology and Management*, **259**, 1003–1008.

Ledig, F.T. & Kitzmiller, J.H. (1992) Genetic Strategies for Reforestation in the Face of Global Climate Change. *Forest Ecology and Management*, **50**, 153–169.

Loarie, S.R., Carter, B.E., Hayhoe, K., Mcmahon, S., Moe, R., Knight, C.A. & Ackerly, D.D. (2008) Climate Change and the Future of California's Endemic Flora. *PLoS ONE*, **3**, e2502.

Mackey, B.G., Berry, S.L. & Brown, T. (2008) Reconciling approaches to biogeographical regionalization: a systematic and generic framework examined with a case study of the Australian continent. *Journal of Biogeography*, **35**, 213–229.

Marris, E. (2009) Planting the forest of the future. *Nature*, **459**, 906–908.

Mbogga, M.S., Hamann, A. & Wang, T. (2009) Historical and projected climate data for natural resource management in western Canada. *Agricultural and Forest Meteorology*, **149**, 881–890.

Mbogga, M.S., Wang, X. & Hamann, A. (2010) Bioclimate envelope modeling for natural resource management: dealing with uncertainty. *Journal of Applied Ecology*, **47**, 731–740.

McKenney, D., Pedlar, J. & O'Neill, G. (2009) Climate change and forest seed zones: past trends, future prospects and challenges to ponder. *Forestry Chronicle*, **85**, 258–266.

Meidinger, D.V. & Pojar, J. (1991) *Ecosystems of British Columbia*. , edn. Special Report Series, No. 6. Research Branch, Ministry of Forests, Victoria, B.C.

Millar, C.I., Stephenson, N.L. & Stephens, S.L. (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications*, **17**, 2145–2151.

O'Neill, G.A., Hamann, A. & Wang, T.L. (2008) Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology*, **45**, 1040–1049.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R.H. & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.

Rehfeldt, G.E. (1994) Genetic structure of western red cedar populations in the Interior West. *Canadian Journal of Forest Research*, **24**, 670–680.

Roberts, D.R. & Hamann, A. (2012) Method selection for species distribution modelling: are temporally or spatially independent evaluations necessary? *Ecography*. DOI 10.1111/j.1600-0587.2011.07147.x. (in press).

Rodrigues, A.S.L., Gregory, R.D. & Gaston, K.J. (2000) Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society B*, **267**, 49–55.

Rose, N.A. & Burton, P.J. (2009) Using bioclimatic envelopes to identify temporal corridors in support of conservation planning in a changing climate. *Forest Ecology and Management*, **258**, S64–S74.

Selby, C.J. & Santry, M.J. (1996) A national ecological framework for canada: data model, database and programs. Centre for Land and Biological Resources Research, Research Branch, Agriculture and Agri-Food Canada and State of the Environment Directorate, Environment Canada, Ottawa, Ont.

Sinclair, S.J., White, M.D. & Newell, G.R. (2010) How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society*, **1**, 5.

Tchebakova, N.M., Rehfeldt, G.E. & Parfenova, E.I. (2009) From vegetation zones to climatypes: effects of climate warming on Siberian ecosystems. *Permafrost ecosystems: Siberian larch forests, ecological studies*, **Vol. 209** (ed. byA. Osawa), pp. 427–446. Springer Verlag, Berlin, Germany. DOI 10.1007/978-1-4020-9693-8_22

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.

Thuiller, W., Albert, C., Araujo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgely, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology Evolution and Systematics*, **9**, 137–152.

Turesson, G. (1925) The plant species in relation to habitat and climate. Contributions to the knowledge of genecological units. *Hereditas*, **6**, 147–236.

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.

Wang, T.L., O'Neill, G.A. & Aitken, S.N. (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications*, **20**, 153–163.

Westfall, R.D. & Millar, C.I. (2004) Genetic consequences of forest population dynamics influenced by historic climatic variability in the western USA. *Forest Ecology and Management*, **197**, 159–170.

Yanchuk, A.D. (2001) A quantitative framework for breeding and conservation of forest tree genetic resources in British Columbia. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **31**, 566–576.

Ying, C.C. & Yanchuk, A.D. (2006) The development of British Columbia's tree seed transfer guidelines: purpose, concept, methodology, and implementation. *Forest Ecology and Management*, **227**, 1–13.

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