Projecting future distributions of ecosystem climate niches: Uncertainties and management applications

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A B S T R A C T

Projecting future distributions of ecosystems or species climate niches has widely been used to assess the potential impacts of climate change. However, variability in such projections for the future periods, particularly the variability arising from uncertain future climates, remains a critical challenge for incorporating these projections into climate change adaptation strategies. We combined the use of a robust statistical modeling technique with a simple consensus approach consolidating projected outcomes for multiple climate change scenarios, and exemplify how the results could guide reforestation planning. Random Forest (RF) was used to model relationships between climate (1961–1990), described by 44 variables, and the geographic distribution of 16 major ecosystem types in British Columbia (BC), Canada. The model predicted current ecosystem distributions with high accuracy (mismatch rate = 4–16% for most ecosystem classes). It was then used to predict the distribution of ecosystem climate niches for the last decade (2001–2009) and project future distributions for 20 climate change scenarios. We found that geographic distributions of the suitable climate habitats for BC ecosystems have already shifted in 23% of BC since the 1970s. Consensus projections for future periods (2020s, 2050s, 2080s) indicated climates suitable for grasslands, dry forests, and moist continental cedar–hemlock forests would substantially expand; climate habitat for coastal rainforests would remain relatively stable; and habitat for boreal, subalpine and alpine ecosystems would decrease substantially. Using these consensus projections and data on the occurrence of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in BC ecosystems, we estimated a twofold increase in seedling demand for this frost-sensitive, commercially important timber species, suggesting managers could begin planning to expand seed inventories and seed orchard capacity to more widely plant this species on logged sites. The results of this work demonstrate the power of RF for building climate envelope models and illustrate the utility of consensus projections for incorporating uncertainty about future climate into management planning. It also emphasizes the immediate need for adapting natural resource management to a changing climate.

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1. Introduction

As the observed ecological impacts of global climate change become increasingly apparent (Dale et al., 2001; Parmesan and Yohe, 2003; Boisvenue and Running, 2006; Parmesan, 2006; Kurz et al., 2008), so has demand for reliable forecasts about how climate change will continue to alter ecosystems. While models projecting ecosystem change have proliferated over the last decade, there remains a keen debate about their accuracy (Pearson and Dawson, 2003; Midgley et al., 2007; Brook et al., 2009) and how natural re-

source managers can best use this information. Model forecasts about climate change impacts on ecosystems can vary substantially, depending on the modeling approach, greenhouse gas (GHG) emission scenario (IPCC, 2007a), and General Circulation Model (GCM) used. Finding ways to reduce uncertainty in forecasts attributable to modeling approaches yet incorporate uncertainty about future GHG emissions and climate into natural resource management planning processes will be key to social, economic and ecological sustainability in a changing climate (Prato, 2008; Trenberth, 2010).

Projections of future ecosystem change can be achieved with either niche-based climate envelope models or process-based mechanistic models. Mechanistic models simulate an array of ecological processes and they have been used forecast changes in ecosystem biomass and productivity as well as changes in geographic

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distribution of vegetation types, species, or ecological zones (e.g., Peng, 2000; Coops et al., 2009; Morin and Thuiller, 2009; Coops and Waring, 2011). The computational complexity and the large data requirements needed to parameterize these models can present challenges for generating accurate forecasts about ecosystem change across vast, mountainous regions (Mohren and Burkhart, 1994; Porte and Bartelink, 2002). Because of this, climate envelope models – also called bioclimate envelope models, or more generally, ecological niche models – have been used more widely to date. They correlate readily available occurrence data with climate variables to model the geographic distribution of realized climate niches for any biological entity (e.g., allele, population, species, ecosystem, vegetation community, natural disturbance, or biome). Climate envelope models of ecosystem change have been criticized for their failure to account for species migration capacity, changes in species interactions, and alterations to biogeochemical cycles, including increased atmospheric CO_2 concentrations (Pearson and Dawson, 2003; Araujo and Guisan, 2006; Austin, 2007; Botkin et al., 2007; Thuiller et al., 2008). While species dispersal considerations are important when the goal is to project actual geographic distributions, climate envelope models do not project actual future ecosystem or species distribution, *per se*, but rather the distribution of climatically suitable habitats, or 'climate niches', which are the target of many ecosystem management activities. As Rehfeldt et al. (2012) recently suggest, the assumption of stable species interactions in ecosystem climate envelope models is only invalidated under novel future climates, and robust methods for incorporating biogeochemical processes are not yet well-developed for either climate envelope or mechanistic modeling approaches. We believe that when the results of climate envelope model projections are appropriately conveyed and used with their limitations in mind, they can provide a powerful framework for evaluating and illustrating potential climate change impacts and guiding land-use planning.

Recent studies demonstrate that substantial variability in projected distributions of future climate envelopes can be attributed to the use of different statistical modeling techniques (Hampe, 2004; Araujo et al., 2005; Heikkinen et al., 2006; Pearson et al., 2006; Dormann et al., 2008; Diniz et al., 2009; Coops and Waring, 2011). To cope with the variable outcomes associated with different statistical techniques, an increasing number of studies implement an approach that fits multiple models and combines them into a consensus forecast (Heikkinen et al., 2006; Araujo and New, 2007; Diniz et al., 2009; Marmion et al., 2009). However, including poor models may compromise the accuracy of projections. The use of multiple models also introduces an additional source of projection variability, which can be substantial (Dormann et al., 2008; Mbogga et al., 2010) and even larger than projection variability generated by the use of different climate change scenarios (Diniz et al., 2009).

Since the accuracy of statistical models can be independently examined, Marmion et al. (2009) recommend that either the most accurate model alone, or a consensus approach combining multiple models that have a good model-fit, be used. In this study, we chose to use a single statistical technique to focus on examining uncertainty in projected future ecosystem distributions associated with a wide range of possible future climates (see below) as the accuracy of climate change scenarios cannot be evaluated and the uncertainty of the future climate is not likely to be reduced (Trenberth, 2010). We used a machine-learning method, Random Forest (RF), to build climate envelope models. RF models were found to be superior to or among the best of a variety of statistical techniques for building climate envelope models (Lawler et al., 2006; Rehfeldt et al., 2006; Elith et al., 2008; Marmion et al., 2009; Attorre et al., 2011; Iverson et al., 2011). They have been used extensively for this purpose in North America (Rehfeldt et al., 2006; Iverson et al., 2008; Rehfeldt et al., 2008; Crookston et al., 2010) and other parts of the world (Lawler et al., 2006; Elith et al., 2008; Attorre et al., 2011).

Uncertainty about future climates presents a challenge both for forecasting the ecological impacts of climate change and for sustainable management of natural resources. Often, projections about climate change impacts are based on a single "mid-range" climate change scenario or small number of GCMs and GHG emission scenario combinations (hereafter referred to as "climate change scenarios") used to represent a wide array of equally plausible future climates (IPCC, 2007b). These strategies reduce computational effort and simplify interpretation for decision-makers; however, relying on only one or few arbitrarily selected climate change scenarios increases the likelihood of producing biased projections. Alternatively, averages of future climate (de Castro et al., 2007; Serrat-Capdevila et al., 2007; Jackson et al., 2011) can be used to make projections; they consider a large number of climate change scenarios without an unmanageable increase in computational effort or complexity. However, with this approach, the individuality of each climate change scenario, in terms of spatial and temporal variation, is lost. To avoid this problem, and to incorporate climate uncertainty in forecasts, we first projected the future distribution of each ecosystem climate niche using each of a selected subset of climate change scenarios separately, then combined the results of multiple projections into a single 'consensus' map on which each pixel is identified as the ecosystem climate most frequently projected across all climate change scenarios.

With an ecological land classification system used widely for natural resource management in British Columbia (BC), Canada, we illustrate ways of reducing and managing uncertainty in projecting the future distributions of climates characterizing BC ecosystems by: (1) using RF to develop a climatic envelope model of contemporary ecosystem distribution; (2) implementing a consensus method to project the contemporary climate envelopes for ecosystems into future climate space; (3) illustrating how variability in projected outcomes due to different climate change scenarios can be conveyed on maps; and (4) exploring how these maps can be used to guide forest management with a case study in reforestation. While climate envelopes for ecosystems can be more challenging to accurately delineate than climate envelopes for their constituent species (e.g., Rehfeldt et al., 2006), there are advantages to projecting shifts in the geographic distribution of ecosystem climate envelopes. In British Columbia, ecosystem units are used as the basis for guiding forest management practices, including selection of the most appropriate trees species used for reforestation. Projections for ecosystems have multiple uses; they can also guide climate change adaptation strategies for other natural resources, such as the conservation of critical wildlife habitat, endangered species habitat, and culturally important ecosystem attributes. Moreover, presence/absence data are not adequate to develop climate envelope models for many species and, therefore, well-delineated ecosystem units can serve as surrogate climate niches for these species. When climate envelopes can be developed for individual species though, they can be used in conjunction with ecosystem projections to guide management (e.g., Rehfeldt et al., 2006; Iverson et al., 2008).

2. Methods

2.1. Ecosystems of British Columbia

The Biogeoclimatic Ecosystem Classification system of BC (Meidinger and Pojar, 1991) divides the province into 16 ecological zones that reflect terrestrial ecosystem differences along large-scale climate gradients related to changes in altitude, latitude

Table 1
Characteristics of ecological zones in British Columbia. All values are averages except area, which is a total.

Ecosystem zone	Latitude N (°)	Longitude W (°)	Elevation (m)	Area (million ha)	MAT[a] (°C)	MAP (mm)	CONT (°)
Boreal Altai Fescue Alpine (BAFA)	57.49	128.66	1685	7.6	−2.5	1101	22.5
Bunchgrass (BG)	50.73	121.11	610	0.3	5.9	342	23.8
Boreal White and Black Spruce (BWBS)	58.17	123.88	719	15.7	−0.3	514	30.3
Coastal Douglas-fir (CDF)	49.04	123.71	73	0.2	9.5	1092	13.9
Coastal Mountain-heather Alpine (CMA)	54.02	128.60	1561	4.4	0.0	3197	19.2
Coastal Western Hemlock (CWH)	51.61	127.01	418	10.8	6.5	2900	15.0
Engelmann Spruce–Subalpine Fir (ESSF)	53.39	122.30	1552	17.2	0.3	1103	22.1
Interior Cedar–Hemlock (ICH)	51.99	120.61	977	5.6	3.2	919	23.0
Interior Douglas-fir (IDF)	50.84	120.89	1019	4.5	3.9	493	22.8
Interior Mountain-heather Alpine (IMA)	51.61	119.01	2261	1.2	−1.6	1570	20.6
Mountain Hemlock (MH)	52.78	127.29	1065	3.6	2.9	3114	17.7
Montane Spruce (MS)	50.85	120.70	1438	2.8	1.8	649	22.0
Ponderosa Pine (PP)	49.88	119.07	643	0.4	6.4	379	23.8
Sub-Boreal Pine–Spruce (SBPS)	52.41	123.86	1152	2.3	1.7	472	22.8
Sub-Boreal Spruce (SBS)	54.35	124.33	900	10.3	2.2	656	23.9
Spruce–Willow–Birch (SWB)	58.44	128.23	1293	8.0	−1.8	691	24.7

[a] MAT = mean annual temperature; MAP = mean annual precipitation; CONT = continentality, the difference between mean warm month temperature and mean cold month temperature with increasing values and indicator of greater continentality.

and continentality (Table 1). These ecological zones cover large geographic areas (up to 172,260 km^2) that are subdivided into increasingly smaller units called subzones and subzone–variants, reflecting plant community composition and structure differences along finer-scale climate gradients. Subzones have distinct regional temperature and precipitation regimes, while subzone–variants are slightly drier, wetter, snowier, warmer, or colder than the average subzone climate. These ecological units are widely used for resource management planning and decision-making in BC.

Ecological zones, subzones, and subzone–variants of BC were mapped by extrapolating the classification of field vegetation plots across landscapes using elevational rules and aerial surveys of physiography (Meidinger and Pojar, 1991). We used the latest version of this map (version 7) (http://www.for.gov.bc.ca/hre/becweb/) to build our climate envelope model of ecosystem distribution in BC. The map, hereafter referred to as the Forest Service ecosystem map, was rasterized to grid resolutions of 1600 m (370,205 cells) and 800 m (1904,654 cells) in ArcGIS (version 9.2) for model building and model validation, respectively. Each cell was assigned to the ecosystem (i.e., zone, subzone, and subzone–variant) occurring at the center of each cell.

2.2. Climate data

We used ClimateWNA (version 4.6) (Wang et al., 2012) to generate climate data. ClimateWNA downscales PRISM grids (2.5 × 2.5 arcmin, ~4 × 4 km) of interpolated monthly temperature and precipitation data (Daly et al., 2002) for the normal reference period 1961–1990 (1970s) to generate point estimates of monthly temperature and precipitation at a finer grid resolution appropriate for analyses of climate change impacts in mountainous regions. ClimateWNA also downscales historical and future climate data, and outputs monthly, seasonal and annual temperature and precipitation variables, as well as derived annual climate variables of biological significance to plants.

To generate the climate data needed for building a model of ecosystem–climate relationships for the 1961–1990 reference period, the elevation of each of the 370,205 cells in a 1600 m grid of the Forest Service ecosystem map was extracted from a 90 × 90 m digital elevation model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM). An input file containing point location coordinates (latitude, longitude, and elevation) for each rasterized grid cell was queried by ClimateWNA to generate 12 annual, 16 seasonal, and 48 monthly climate variables for each grid cell. The same procedures were followed using 1,904,654 cells in

a 800 × 800 m grid to generate climate data for: (1) the reference period to validate our model, (2) the last decade (2001–2009) to assess the effects of recent climate change, and (3) three future periods (2020s, 2050s and 2080s) to project impacts of future climate change. For climate data spanning 2001–2009, we calculated averages for each climate variable over the 9 years in that period.

To address the issue of uncertainty in projected future ecosystem distributions due to climate change scenarios, we selected scenarios to represent the range and distribution of equally plausible future climates. We considered the variation in projected future climates for GHG emission scenarios (A2, B1, and A1B), GCMs, and model runs for each GCM simultaneously, plotting projected changes in mean annual temperature and precipitation from 133 such combinations for 2050s. A Regional Analysis Tool developed by the Pacific Climate Impact Consortium (http://www.pacificclimate.org) was used to assist with this analysis. We selected 20 climate change scenarios (Table 2 and Fig. 1), of which 10 were recommended for climate change analyses in BC to represent the range of the temperature–precipitation combinations (Murdock and Spittlehouse, 2010). Another 10 were selected randomly to represent the distribution with modification to avoid inclusion of highly similar scenarios. In total, the model runs yielded 60 projections (i.e., three future periods × 20 climate change scenarios) of the future distribution of ecosystem climate envelopes.

Table 2
The 20 climate change scenarios selected from 133 IPCC Fourth Assessment scenarios available at the Pacific Climate Impact Consortium. Scenarios 1–10 were recommended by Murdock and Spittlehouse (2010) to represent the range of the variation among all the scenarios. Scenarios 11–20 were selected randomly to represent the distribution.

Scenarios representing the range of future climates	Randomly selected scenarios
1. cccma_cgcm3_A2-run4	11. bccr_bcm20_A2-run1
2. cccma_cgcm3_A2-run5	12. cccma_cgcm3_B1-run2
3. csiro_mk30_B1-run1	13. cccma_cgcm3_B1-run5
4. gfdl_cm21_A2-run1	14. mri_cgcm232a_A2-run1
5. giss_eh_A1B-run3	15. mpi_echam5_A1B-run2
6. mpi_echam5_B1-run1	16. ipsl_cm4_A1B-run1
7. mri_cgcm232a_B1-run5	17. giss_eh_A1B-run2
8. ncar_ccsm30_A1B-run5	18. gfdl_cm21_A1B-run1
9. ukmo_hadcm3_B1-run1	19. miroc32_medres_A2-run2
10. ukmo_HadGEM1_A1B-run1	20. miroc32_Hires_B1_run1
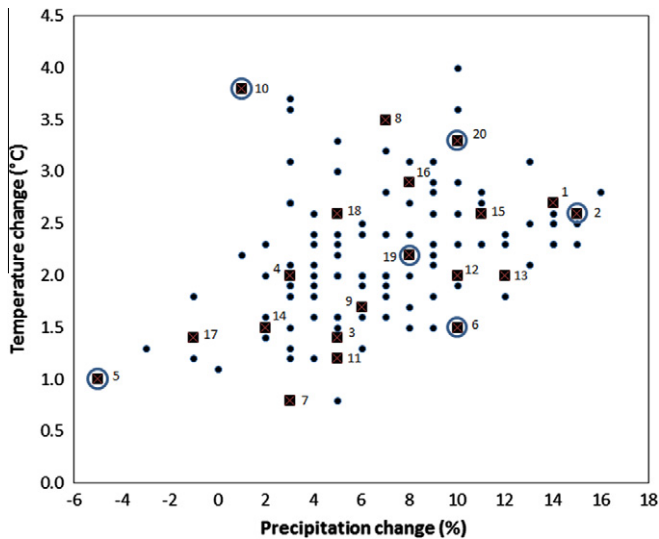
Fig. 1. Scatterplot of the changes in mean annual temperature and mean annual precipitation from the reference period (1970s) to 2050s, for 133 climate change scenarios available in the Pacific Climate Impact Consortium Regional Analysis Tool (http://www.pacificclimate.org). The 20 climate change scenarios used in the consensus analysis are shown as squares (■). The scenario representing the mean expected change in climate and the five scenarios representing the range of climatic projections (see Fig. 6) are shown as circled squares (⊡). Numbers beside the selected scenarios are consistent with the numbers in Table 1.

2.3. Modeling relationships between climate and ecosystem distribution

We used the R version (Liaw and Wiener, 2002) of Breiman's (2001) Random Forest (RF) algorithm to model relationships between climate for the 1970s reference period and the geographic distribution of ecosystems in BC. RF produces many classification trees, collectively called a 'forest', and aggregates the results over all trees. Each of these decision trees in the forest is constructed using a bootstrap sample of the input data (i.e., a random sample with replacement) so that the resulting dataset ('bagged sample') contains about 64% of the original observations, and the remaining observations comprise the 'out-of-bag' (OOB) sample. Tree nodes (bifurcations in a branch) are created using the climate predictor variable that has the smallest classification error among a randomly selected subset of predictor variables. By default, the number of predictors randomly selected at each node is the square root of the total number of predictors. Using the trees grown with the bootstrap sample, each of the independent observations in the OOB sample is classified (assigned to an ecosystem) and a model prediction error, called the OOB error (% of incorrectly classed observations), is calculated.

To calibrate the model, we compared OOB prediction errors for models using four different sets of climate variables: (1) 12 annual variables, (2) 16 seasonal variables, (3) 48 monthly variables; and (4) all 76 climatic variables. The variable set with the lowest OOB error was used to build the model. The number of predictors selected at each node was optimized using the function *tuneRF*. RF was run with 200 classification trees; use of a larger number of these decision trees did not reduce OOB error. For the model that included all 76 climate variables, importance values (as determined by a decrease in Gini values, see Breiman, 2001) generated by RF were used to reduce the number of climate variables included in the model without compromising model accuracy.

The RF model was built at the subzone–variant level and results were summarized at the ecosystem zone level. As subzone–variants differed greatly in geographic area, using all grid cells (observations) in the grid generated small samples for small

subzone–variants, which resulted in their being poorly modeled. We reduced OOB errors for smaller subzone–variants by increasing their relative representation through reducing sampling intensity for larger subzone–variants having more than 2000 observations using a graduated sampling strategy. The number of randomly sampled data points (n_i) was calculated as follows:

$$n_i = 2000 + [n(\ln(10^5/n)/10) - 780] \qquad (1)$$

where n is the total number of data points in a subzone–variant. After model calibration, OOB errors for the final RF model were compared to prediction errors of a previous model (Hamann and Wang, 2006), which used discriminant analysis to predict ecosystem class from climate variables. We chose the subzone–variants having 2000 observations as the threshold to apply gradual sampling because the OOB errors were considerably larger for the subzone–variants having less than 2000 observations.

The RF model was validated by comparing BC ecosystem maps predicted using 800 m grid climate datasets for the reference period (1960–1990) with the BC Forest Service ecosystem map. Model fit (observed vs. predicted) was quantified with pixel-by-pixel comparison of ecosystem class. Mismatch rate (%) was calculated as the percentage of observations where the predicted ecosystem unit in RF differed from the observed ecosystem unit on the Forest Service ecosystem map.

2.4. Assessing effects of climate change on ecosystem climate niche distributions

To assess the impact of recent climate change on ecosystem, we compared predictions of ecosystem climate niches for the reference period 1961–1990 with predictions for 2001–2009. Future impacts were similarly quantified by comparing ecosystem climate niches projected for future periods (2020s, 2050s and 2080s) with the reference period. Shifts in geographic distributions of ecosystem climate niches were used to estimate the loss and gain of areas of suitable climate for each ecosystem unit. Model output was gridded and mapped at 800 m resolution.

To consolidate variation in projected ecosystem climate niches among the 20 selected climate change scenarios, we generated a single consensus map for each of the three future climate periods by mapping the climate niches for the subzone–variant most frequently projected for each pixel. Assuming the degree of agreement among projections reflects the level of certainty about future ecosystem type, we produced additional maps showing the degree of consensus among scenarios as measured by the frequency (%) with which an ecosystem class was projected for a map pixel. Similarly, for each future time period, we mapped whether a pixel was projected to have remained within the climate envelope of the same ecosystem unit or shifted to another ecosystem's climate niche since the 1970s, according to the frequency of votes for ecosystem change among all 20 scenarios. Together, these maps provide natural resource managers in BC with an indication of the regions that are likely to experience the most change, what those changes will be, and a measure of confidence regarding that change. To illustrate the effect that different climate change scenarios had on projections of future ecosystem climate niches, we mapped future climate envelopes for ecosystem zones using five extreme and one middle-of-the-road climate change scenario for the 2050s (see Fig. 1).

2.5. Case study: ecosystem climate niche shifts and reforestation with Douglas-fir (Pseudotsuga menziesii)

Few studies provide examples of how projections about shifts in ecosystem climate niches can be incorporated into natural re-

source management planning. Given BC's ecosystem classification is used to guide the selection of native tree species planted after logging, we exemplified the utility of our consensus projections for estimating the number of Douglas-fir (*P. menziesii* [Mirb.] Franco) seedlings needed for future reforestation. Douglas-fir is among the most valuable timber species in BC; approximately 15 million seedlings are planted annually for the two varieties of Douglas-fir: Coastal Douglas-fir (*P. menziesii* var. *menziesii*) is widely planted in the maritime CWH zone, and interior Douglas-fir (*P. menziesii* var. *glauca*) is planted in several zones with continental climates (primarily in the ICH, IDF, and SBS zones, with limited use in the MS, BWBS and SBPS zones).

We predicted the distribution of Douglas-fir's climate envelope for the reference period (1961–1990), and the 2020s, 2050s and 2080s following Hamann and Wang (2006). The frequency of major species in BC including Douglas-fir has been estimated for each ecosystem unit (subzone–variant) (Hamann et al., 2005). Through associating the frequency of Douglas-fir for each ecosystem unit with RF consensus projections of ecosystem climate niche distribution, we projected the climate envelope for this species in future periods. Our climate envelope for Douglas-fir corresponded well to Little's (1978) published range map indicating strong climatic controls on its geographic distribution. Assuming stable forest harvest rates, the average number of Douglas-fir seedlings annually planted per hectare in each subzone–variant from 2000 to 2010 was multiplied by the projected areal extent (ha) of each subzone–variant climate niche in the future to estimate the number of seedlings needed to reforest logged sites. Changes in seedling demand relative to present were calculated for the projected future distribution of ecosystem climate envelopes. This example provides a tangible indication of the implications of climate change for Douglas-fir reforestation for foresters, seed collectors, seed orchards, and seedling nurseries.

3. Results

3.1. Random Forest model

Use of all 76 climate variables, rather than separate sets of climate variables (i.e., annual, seasonal, or monthly), yielded the lowest OOB error (Fig. 2). However, to produce the most parsimonious model, the number of climate variables included in the final model was reduced based on importance values to a subset of the most influential variables (27 monthly, 13 seasonal, and 4 annual climate variables), without significantly increasing OOB error (Table 3). Reducing the sample size drawn from geographically large subzone–variants in a non-linear fashion (Fig. 3a) reduced OOB error substantially for 83% of ecosystems (smaller ones with <8000 data points) but increased it slightly for large ones (with >8000 data points) (Fig. 3b), resulting in an overall reduction in the average OOB error across all ecosystems. The final RF climate envelope model used 44 climate variables – from which 12 (the optimized number determined by *tuneRF*) were randomly selected at each node of a decision tree and 200 classification trees.

Model errors of fit (mismatch rates) were low (4–16%) for all ecosystems except the three alpine ecosystems (CMA, BAFA, and IMA) and the subalpine Mountain Hemlock (MH) ecosystem (21–32%) (Table 4). There was a near perfect correspondence of the RF predicted map with the BC Forest Service ecosystem map for the low and mid-elevation zones (Fig. 4a and b). A possible explanation for high mismatch rates among some high-elevation ecosystems was revealed using finer resolution RF model runs (based on 90 m DEM from SRTM) for coastal BC. High prediction errors for the Coastal Mountain-heather Alpine (CMA) and MH were mostly because the model was unable to discriminate between the MH
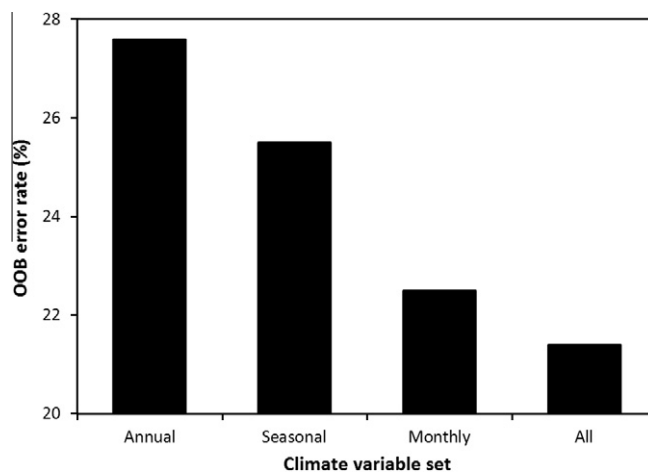

Fig. 2. Out-of-bag (OOB) error rates for Random Forest models for predicting ecological subzone–variants using only annual, seasonal, or monthly climate variables, or all climate variables together.

and CMA zones, which occur in elevational sequence below and above treeline, respectively (Fig. 5a and b). When the Forest Service ecosystem map and the predicted distributions of these ecosystems were superimposed onto a satellite image, we observed that the areas mapped by the Forest Service as CMA but predicted to be MH by the RF model, were generally forested and thus subalpine (MH), not alpine (CMA). This suggests that the majority of classification errors near treeline in these zones result from mapping rather than our modeling approach, and the high mismatch rates do not necessarily mean our models predict these high-elevation ecosystems poorly. Less frequent sampling of these high-elevation zones and different methods used to delineate the treeline boundary likely contributed to their apparent mis-classification on the BC Forest Service ecosystem zone map.

Our calibrated RF model correctly predicted ecosystem class from climate variables more frequently than the discriminant analysis techniques used by Hamann and Wang (2006), indicating the RF model was more accurate. OOB prediction errors for the calibrated RF model were 12% lower than prediction errors produced by the discriminant model for the ecological zones, and 35% lower for the subzone–variants (Fig. 6).

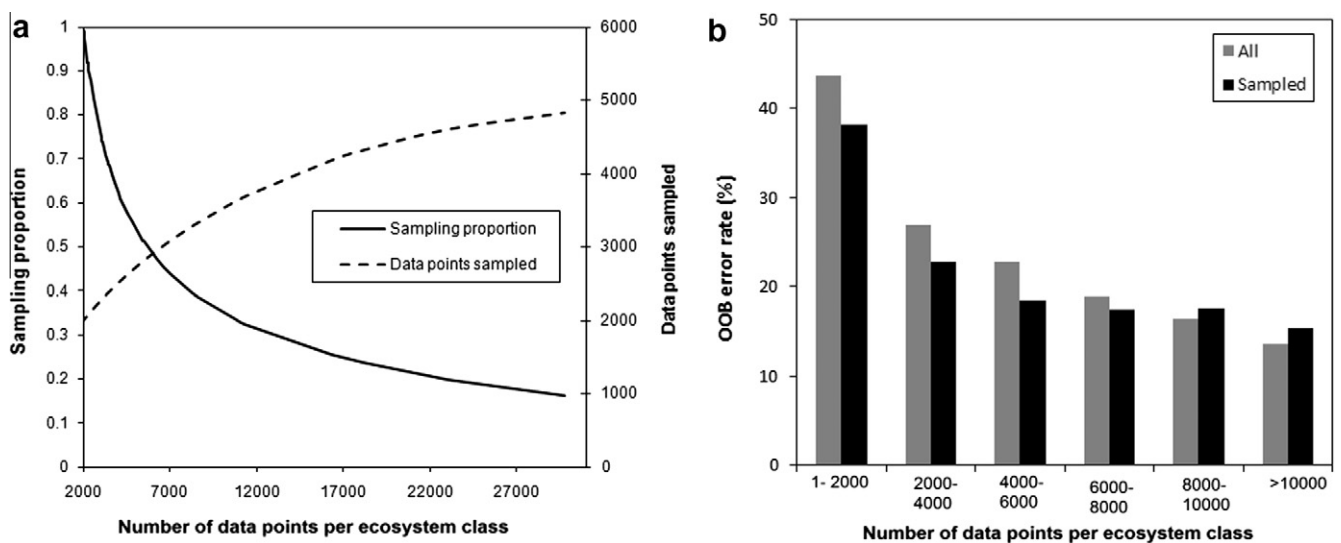### 3.2. Shifts in ecosystem climate niche

Based on a comparison of mapped predictions of ecosystem distributions for the 1970s and for 2001–2009, we calculated that about 23% of the geographic area of BC has already shifted to climates characteristic of different ecosystem zones (Fig. 4 b and c). The magnitude of the shift (loss or gain) varied between 5% and 77% among ecosystems. The most affected ecosystems included some high-elevation ecosystems (IMA and MS) and sub-boreal ecosystems (SBPS and SWB). The loss of their suitable climate ranged from 46% to 59% of their total area. Substantial range expansions (between 51% and 77%) were projected for some ecosystems, including Interior Douglas-fir (IDF), Ponderosa Pine (PP), Bunchgrass (BG) and Interior Cedar Hemlock ecosystem (ICH) zones. Most of these (IDF, PP and BG) are dry ecological zones. The least affected were two coastal (CDF and CWH) and one boreal zone (BWBS).

Consensus projections of ecosystem distribution (Fig. 4d–f) suggest that impacts on BC ecosystems will intensify as climate change accelerates in future periods. Vulnerability to a changing climate was projected to differ substantially among ecosystems (Table 5 and Fig. 4). By the end of the century, loss of area covered

Table 3
Climate variables selected from a total of 76 tested for inclusion in the final Random Forest model and their importance values (decrease in Gini values). Prec = precipitation, T_{max} = maximum temperature, T_{min} = minimum temperature, T_{ave} = average temperature, sp = spring (March–May), sm = summer (June–August), at = autumn (September–November), wt = winter (December–February), Continentality (TD) = (mean warmest month temperature) – (mean coldest month temperature), SHM = summer heat-moisture index, EMT = extreme minimum temperature and PAS = precipitation as snow.

| Climate variable	Importance value	Climate variable	Importance value	Climate variable	Importance value	Climate variable	Importance value
TD	7696	Tmax_sm	5608	Tmax10	5120	Tmax07	4561
Prec10	7298	Prec_sp	5588	Prec11	5078	Tmin10	4513
Tmin11	6219	Prec05	5550	Tmin_wt	5027	SHM	4513
Prec06	6155	Prec09	5502	Prec01	4983	Tmax08	4458
Prec12	5953	Prec_at	5478	Tmin02	4981	Tmin06	4321
Tmax02	5901	Prec07	5379	Prec03	4978	Tmin05	4315
Tmin_sm	5821	Tmax11	5347	Tave_sp	4942	Tmax09	4185
Tmax_sp	5815	Prec_wt	5311	Tmax05	4779	Prec02	4178
Prec08	5762	Tave_sm	5268	Tmax01	4760	EMT	4077
Tmax_wt	5692	Tmax_at	5217	Tmin12	4746	Tmin01	3945
Prec_sm	5611	Prec04	5193	Tmin_at	4682	PAS	3873

Fig. 3. A strategy for sampling the input dataset used to build the Random Forest model (a) and its effects on out-of-bag (OOB) error rate for ecosystem class (subzone–variant) of various sizes. The number of data points per ecosystem class indicates its relative size (b).

Table 4
Comparison of the current British Columbia Forest Service map of ecological zones with a map of climate envelopes predicted by Random Forest. Accuracy of the predicted map was measured by a pixel-by-pixel comparison of ecosystem zone classification on the Forest Service map and the predicted map (i.e., mismatch rate) using an independent dataset at a higher resolution than that used in building the model. Degree to which the predicted map varies from the BC Forest Service map is described by changes to the following zone features: area, elevation, and northern position.

Ecosystem zone	Mismatch rate (%)	Difference between predicted and BC Forest Service ecosystem maps		
		Area (%)	Elevation (m)	Northern position (km)
BAFA	24	−11	27	19
BG	16	−4	−8	−1
BWBS	4	−1	−1	1
CDF	5	−1	−2	−1
CMA	32	−21	89	36
CWH	10	−4	−25	1
ESSF	10	6	4	6
ICH	13	−2	−20	8
IDF	8	−1	−3	1
IMA	30	−8	21	1
MH	21	42	32	−2
MS	14	2	−4	0
PP	16	2	−6	0
SBPS	6	0	−3	1
SBS	6	−1	−5	4
SWB	16	0	0	4

Note: Elevation and northern position were measured as averages of ecological zones within British Columbia. Positive values for area, elevation and northern position indicate expansion, upward and northern movement, respectively.
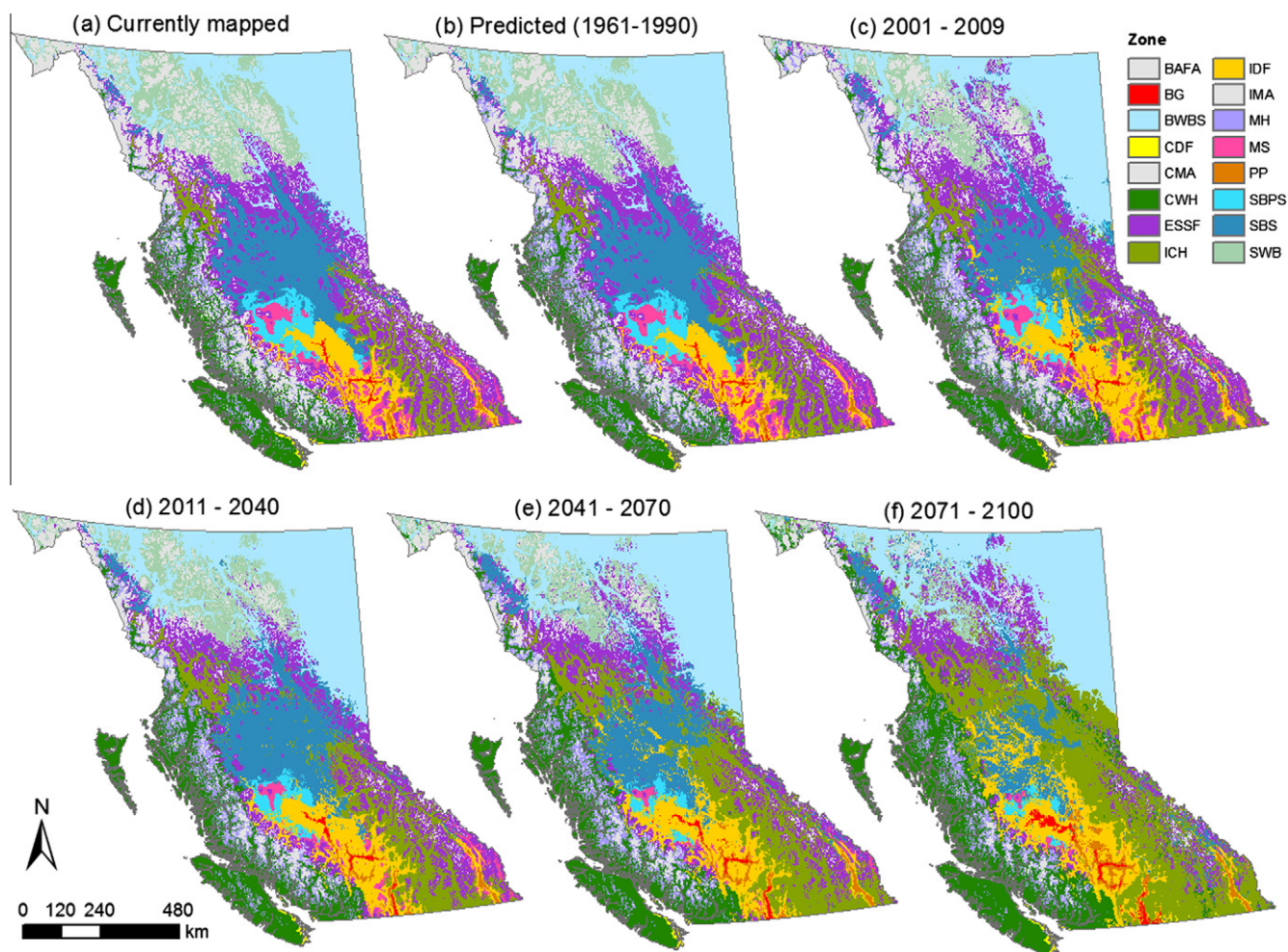
Fig. 4. Geographic distributions of ecological zones currently mapped (a), predicted (1961–1990) (b), and their projected climate envelopes for current (2001–2009) (c), 2020s (d), 2050s (e), and 2080s (f) based on consensus predictions with the best-model agreement among 20 selected climate change scenarios. The projections can be visualized and downloaded at http://www.genetics.forestry.ubc.ca/cfcg/ClimateBC40/Default.aspx
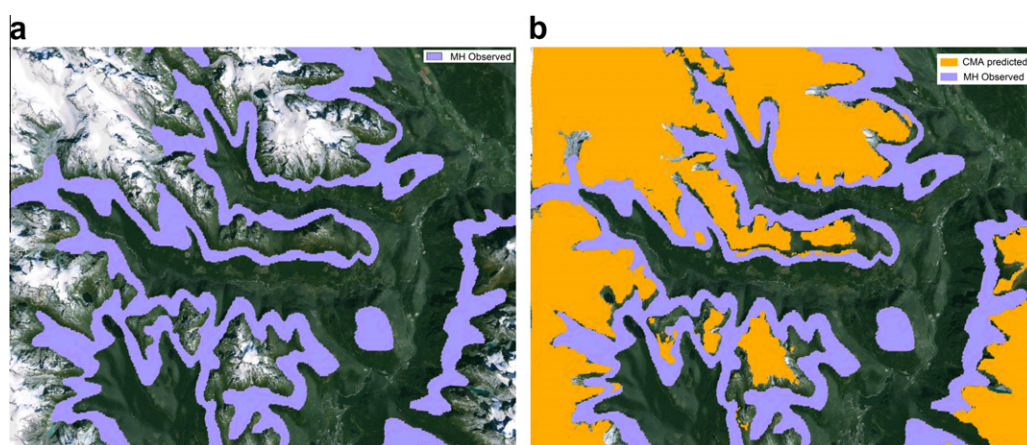

Fig. 5. Distributions of Mountain Hemlock (MH) zone and predicted climate envelope for the Coastal Mountain-heather Alpine (CMA) zone for the reference period (1961–1990) superimposed onto a satellite image for a region of southern British Columbia (centered at Lat. 50°18′N and Long. 123°02′W). The CMA zone occupies areas above the MH zone in (a) or predicted CMA zone plus the gaps between the predicted CMA and the MH zones in (b). The gaps are mostly forested areas and predicted to be MH zones.

by ecosystem climate envelopes for the reference period (1961–1990) was projected to range from 2% to 96% (mean = 56%), and ecosystem climate envelopes were projected to shift 70–455 m (mean = 209 m) upward in elevation and 2–278 km northward

(mean = 84 km northward) (Table 5). High-elevation (BAFA, IMA and MS) and sub-boreal ecosystems (SBPS, SBS and SWB) were most vulnerable and over 80% of the area covered by their climate envelopes was projected to be lost by the end of the century. In
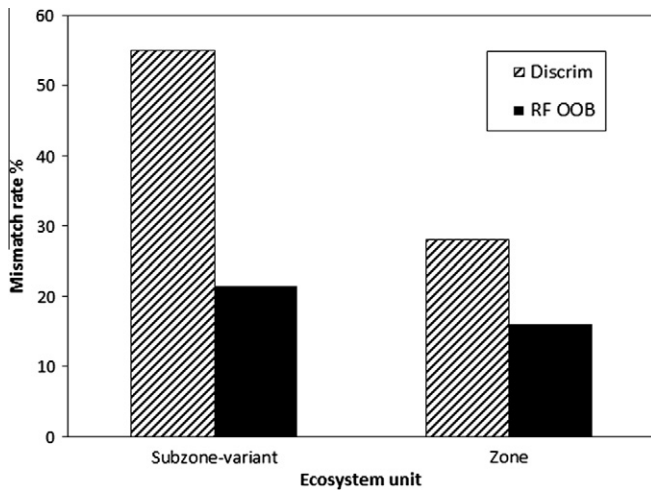
Fig. 6. Comparisons in pixel-by-pixel mismatch rates (%) between the current Forest Service ecosystem map and predicted maps of ecosystem climate habitats produced using different statistical approaches to modeling climate–ecosystem relationships: Random Forest (RF) and discriminant analysis (Discrim) (see Hamann and Wang 2006, for details of discriminant analysis). RF OOB = Random Forest model predictions using out-of-bag data points (independent predictions).

contrast, the area covered by climate envelopes for grasslands (BG), dry forested ecosystems (PP and IDF) and Interior Cedar Hemlock ecosystems (ICH) were projected to expand, with the area predicted to have interior rainforest (ICH) climates expanding three-fold and becoming the most common climate type in BC by 2080. The extent of low elevation boreal (BWBS) and coastal (CWH and CDF) ecosystems was projected to remain relatively unchanged.

Confidence in consensus projections about future ecosystem climate niche distribution varied over time and space (Fig. 7a–c). Consensus was moderate to strong in the 2020s, with agreement on projected ecosystem averaging 66% across all pixels. By the 2080s, projections became less certain with average consensus of projected ecosystem for a pixel declining to 51%. Future ecosystem climate niches were projected with greatest confidence in northeast BC and along parts of the coast. Only relatively small areas of BC were projected to remain unchanged by 2080 (Fig. 7d–f).

The range of climate change impacts on ecosystem climate niches was examined by comparing the predicted reference period (1961–1990) ecosystem distribution (Fig. 4b) with projections based on five extreme and one middle-of-the-road climate change scenarios (Fig. 8). For example, by 2050, climates characterizing the SWB boreal ecosystem of northern BC (Fig. 4b) were largely replaced by more southern subalpine climates (ESSF) under the middle-of-the-road climate change scenario 19 (~2 °C temperature increase and ~8% precipitation increase) (Fig. 8). Under the hottest scenario (scenario10: ~3.7 °C temperature increase and unchanged precipitation), the SWB climate was replaced by the climates of either the subalpine ecosystem ESSF or the sub-boreal ecosystem SBS (Fig. 8). Similarly, by 2050, the geographic extent of the temperate rainforest climate associated with Interior Cedar Hemlock (ICH) ecosystems is projected to expand over much of southern BC, but only under scenarios projecting temperature increases >~2.5 °C (e.g., scenarios 2, 20, 10), reaching their greatest extent under scenarios projecting increases in precipitation around 10% (e.g. Fig. 8, scenario 20). The extent of hot, dry climates typical of BG, PP, and IDF ecosystems nearly double and alpine climates virtually disappear by the 2050s under extreme warming scenarios projecting increases over ~3.3 °C (e.g., Fig. 8, scenario 10).

3.3. Case study: projected changes in seedling requirements for reforestation

We projected substantial expansion of the geographic area with suitable climate for Douglas-fir in future periods (Fig. 9). Such expansions were projected to occur throughout coastal and southern BC, resulting in doubling of the total area potentially suitable for this species at the end of the century. Consequently, we projected a corresponding increase in Douglas-fir seedling demand for reforestation by 110%, 160% and 220% by the periods 2020s, 2050s and 2080s, respectively, relative to the average number of seedlings (about 15 million) planted annually over the past 11 years (2000–2010) (Fig. 10). This estimate assumes current rates of logging and reforestation continue, and no major changes in silvicultural practices occur. These increases were mainly attributable to the expansion of the geographic area of climate envelopes for CWH, ICH and IDF ecosystems, in which Douglas-fir is currently used as a major species for reforestation. The planting of the coastal variety is projected to increase by 340% (CWH only), while plant-

Table 5
Predicted shifts in climate envelopes for ecological zones for the current (2001–2009) and projected shifts based on the consensus among the 20 selected climate change scenarios listed in Table 2 and three future periods 2020s (2011–2040), 2050s (2041–2070) and 2080s (2071–2100) relative to the reference period (1961–1990). Loss indicates the percent decrease in area of a mapped zone due to pixels that now have or are projected in the future to have climates outside of the climatic envelop of that zone. Gain indicates the percent increase in area of a zone due to pixels mapped in other zones that have climates that fall within the climatic envelope of the zone. Zone abbreviations are shown in Table 1.

Ecosystem zone	Loss/gain/change of climate habitat (%)				Elevation shift (m)				Northward shift (km)			
	Current	2020s	2050s	2080s	Current	2020s	2050s	2080s	Current	2020s	2050s	2080s
BAFA	−31/13/−18	−48/1/−47	−66/2/−64	−81/0/−81	21	80	119	170	10	41	70	95
BG	−39/66/27	−38/57/19	−43/114/71	−49/117/128	30	0	97	186	12	4	14	14
BWBS	−8/7/−1	−3/16/13	−7/19/12	−10/21/11	11	52	59	70	2	2	12	18
CDF	−5/24/19	−15/14/−1	−19/16/−3	−22/41/19	9	16	24	128	5	−3	−6	10
CMA	−18/29/11	−29/13/−16	−44/18/−26	−60/15/−45	15	90	143	208	16	53	94	138
CWH	−5/13/8	−2/24/22	0/40/40	−2/71/69	49	105	191	323	7	18	36	69
ESSF	−21/27/6	−34/15/−19	−59/38/−21	−74/41/−33	−15	103	119	123	104	54	174	278
ICH	−20/51/31	−7/83/76	−6/206/200	−10/335/325	63	144	212	260	31	26	79	127
IDF	−11/77/66	−13/55/42	−22/100/78	−39/130/91	52	89	86	72	38	22	75	126
IMA	−49/31/−18	−54/2/−52	−76/2/−74	−81/0/−81	−113	150	223	246	162	7	28	38
MH	−23/30/7	−33/29/−4	−70/63/−7	−74/62/−12	25	176	286	455	54	28	55	75
MS	−59/32/−27	−64/20/−44	−90/15/−75	−96/8/−88	89	142	251	312	33	3	35	105
PP	−38/67/29	−25/86/61	−37/152/115	−41/252/211	6	85	152	235	25	16	34	77
SBPS	−55/35/−20	−67/22/−45	−86/15/−71	−93/8/−85	61	116	178	190	27	5	2	−2
SBS	−31/21/−10	−19/30/11	−52/37/−15	−80/36/−44	21	47	101	154	27	18	63	145
SWB	−46/11/−35	−36/23/−13	−71/22/−49	−88/14/−44	46	129	159	212	2	0	17	23
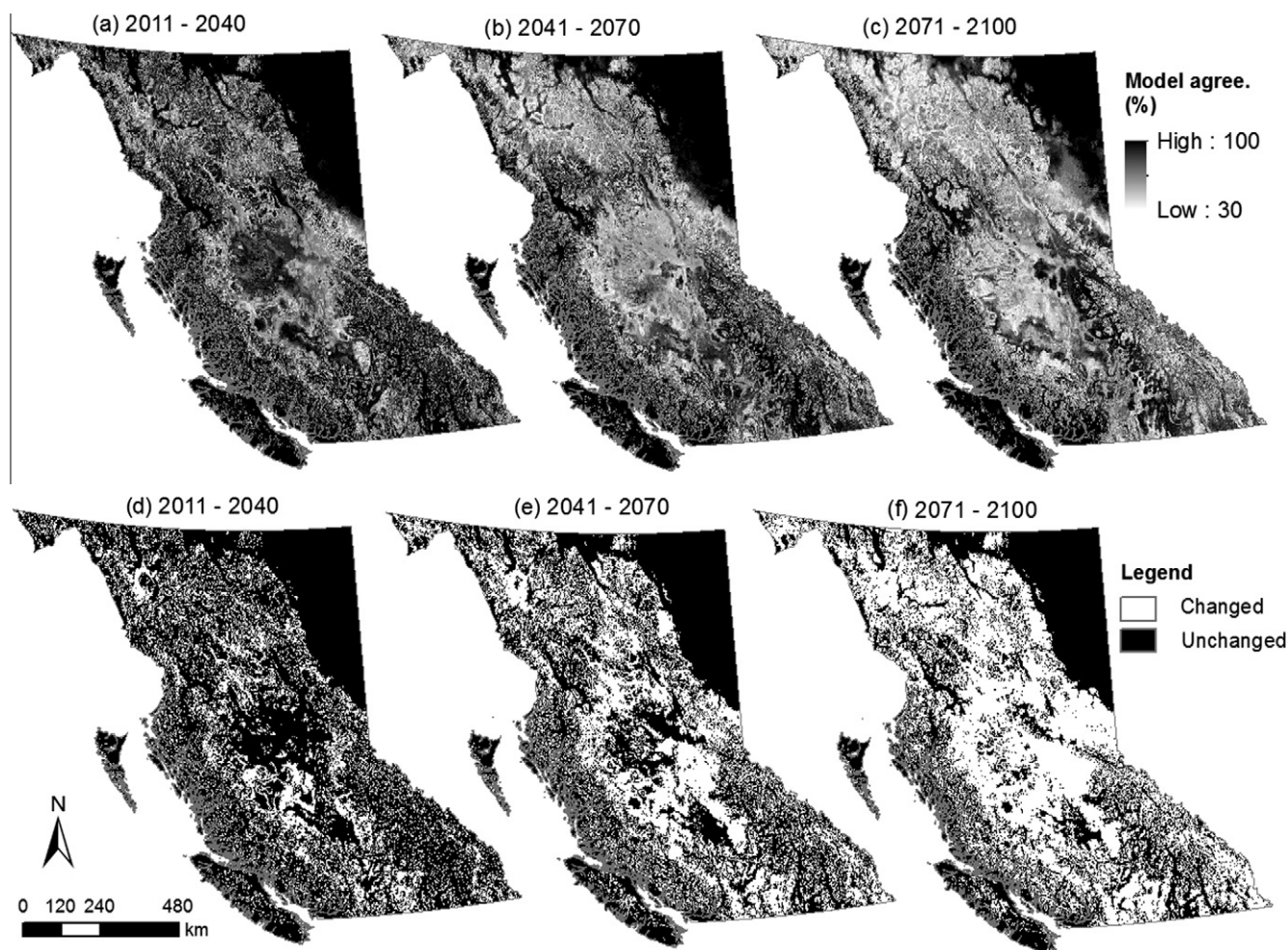
Fig. 7. Geographic distributions of model-agreement (consensus strength) among the 20 projections of ecological zones based on the 20 selected climate change scenarios for (a) 2020s, (b) 2050s and (c) 2080s. Also shown are areas with unchanged ecosystem zone climate habitats for the same periods ((d)–(f), respectively).

ing of the interior variety is projected to increase by 170% (all other zones) at the end of this century. In other zones, the predicted increase in potential planting rates are relatively low, but those zones do not account for much of the total Douglas-fir planting in the province.

## 4. Discussion

4.1. Model accuracy

The accurate predictions of BC ecosystem climatic envelope distributions using Random Forest (RF) support previous reports on the strong performance of RF models (Lawler et al., 2006; Rehfeldt et al., 2006; Elith et al., 2008; Marmion et al., 2009; Attorre et al., 2011). The accuracy of RF models is largely because the method exploits two sources of randomness: random bootstrap input of observations (bagging) used to build the model, and splitting of classification tree nodes using a random subset of predictors, thus overcoming the collinearity and over-fitting problems of other statistical techniques (Breiman, 2001; Liaw and Wiener, 2002; Prinzie and Van den Poel, 2008). Moreover, RF is an ensemble classifier, which means it aggregates predictions across many classification trees, generating more robust predictions than most single-tree methods (Breiman, 2001; Cutler et al., 2007).

In most cases, annual climate variables are used to build climate envelope models with RF. However, we found that the accuracy of

our RF model could be improved by including seasonal and monthly variables, suggesting that the seasonal and monthly climate patterns are also important to predict ecosystem climate niches. Partially balancing sample sizes among classes also improved the model because it struck a balance between the need to have somewhat more samples in geographically large ecosystems than small ones (to adequately deal with greater spatial heterogeneity in climate across large ecosystems) and the need to increase relative sample sizes of small ecosystems.

4.2. Climate change and geographic shifts in ecosystem climates

Predictions based on weather instrument records from 2001 to 2009 indicated that 23% of the climate envelopes for ecosystems have already shifted to another ecosystem's climate since the 1970s. The magnitude of this change was surprising; it was essentially equal to changes projected for the 2020s despite average temperature increases for 2001–2009 being smaller (0.71 °C) than projected increases for the 2020s (1.17 °C). This is probably because increased temperature during 2001–2009 was not accompanied by increased precipitation (−0.5%) – as the expansion of grassland (BG) and dry forest climates would suggest – while the GCMs used for 2020s projections on average included an increase in precipitation (averaging 3.3% over the 20 climate scenarios, Fig. 1). We acknowledge that decadal-term climate data can deviate from normal (30-year) data due to shorter-term climatic vari-
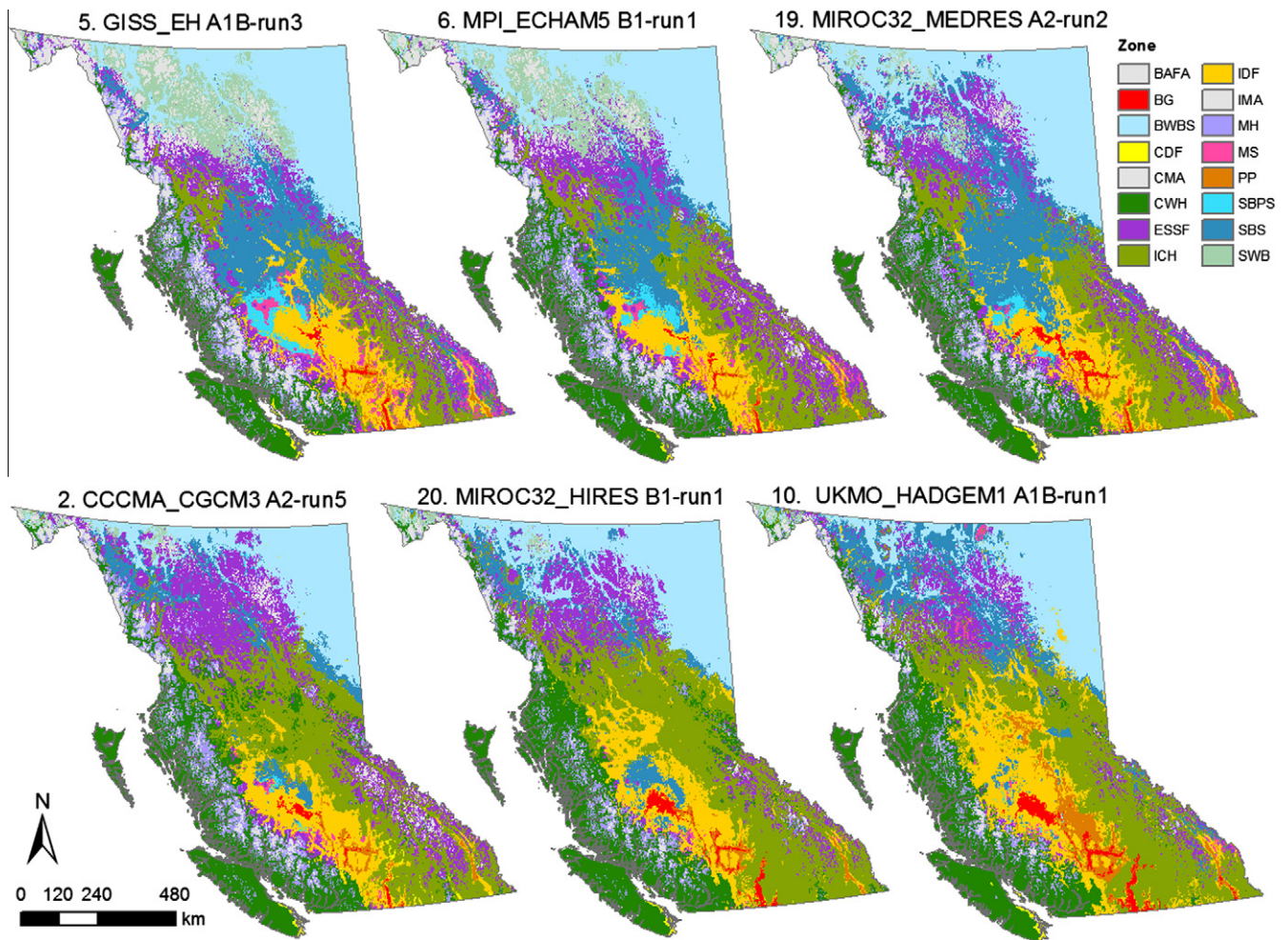
Fig. 8. Projected distributions of climate envelopes of British Columbia's ecosystems for a climate change scenario of average magnitude (MIROC32_MEDRES A2-run2) and for five extreme climate change scenarios for the 2050s. Climate change scenarios are shown above each map and are listed in Table 2. The relative magnitude of climate change for each scenario is shown in Fig. 1.

ability other than anthropogenic climate change, such as that due to the Pacific Decadal Oscillation (PDO), may have affected climate during this period (2001–2009). However, the average PDO indices are about the same for the reference period (−0.0619) and this period (−0.0625) based on the data provided by the University of Washington (http://jisao.washington.edu/pdo/), suggesting the difference in climate between these two periods is not directly attributable to the PDO effect.
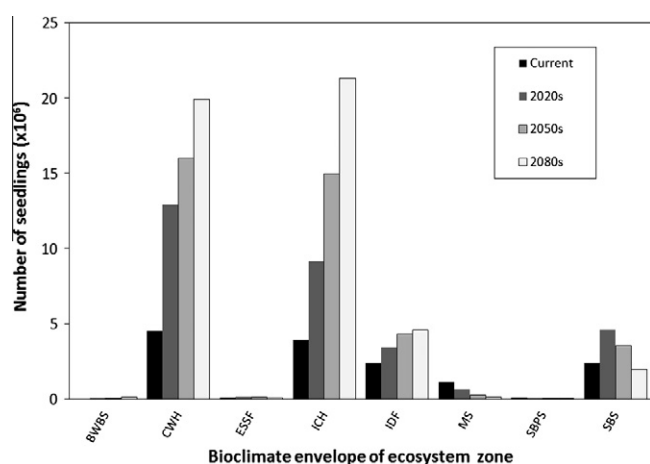
Our consensus projections indicate potential for substantial shifts in the geographic distribution (i.e., location and extent) of most BC ecosystem climate niches over the next century. The climate envelopes for relatively productive, mild interior Cedar–Hemlock (ICH) forests, interior Douglas-fir (IDF) and Coastal Western Hemlock (CWH) rainforests were projected to expand over much of BC at the expense of climate envelopes for less productive sub-boreal, subalpine, and alpine ecosystems. These changes suggest British Columbia could contribute to increased forest productivity and carbon sequestration through reforestation activities, provided suitable tree species and populations are planted to match up with the new climatic conditions (Aitken et al., 2008). Such opportunities may not be common on a global scale as terrestrial ecosystems become net carbon sources due to widespread forest dieback and more severe natural disturbances, which provide a positive feedback to global warming (Scholze et al., 2006; Heimann and Reichstein, 2008; Finzi et al., 2011).

Our projections of potential future ecosystem climate are broadly consistent with other RF model projections developed over larger-scales for western Canada (Mbogga et al., 2010), the western USA (Rehfeldt et al., 2006) and North America (Rehfeldt et al., 2012). All models projected the expansion of climates supporting grasslands, dry forests and interior wet forests; major reductions in the distribution of colder montane climates supporting alpine and subalpine ecosystems; and relative stability of the extent of coastal temperate rainforest climates. Our projections differed most notably from Mbogga et al. (2010) and Rehfeldt et al. (2012) in the boreal forest region of northeastern BC (BWBS). While we projected little change in the distribution of boreal climates of northern BC, the RF model of Mbogga et al. (2010) projected a large proportion of BWBS being replaced by temperate dry forest typical to southern Alberta; Rehfeldt et al. (2012) projected a northwestward expansion of the cool temperate steppe climates (typical of the central United States) into the current BWBS zone. These discrepancies can likely be attributed to our model projections being constrained to ecosystems currently present in BC, which limited our ability to account for the expansion of climates from surrounding regions. However, differences in ecosystem classifications between BC and Alberta, as well as different climate change scenarios, RF model calibrations used and projection scales, may also explain why our projections for northern BC depart from those produced by Mbogga et al. (2010) and Rehfeldt et al. (2012).
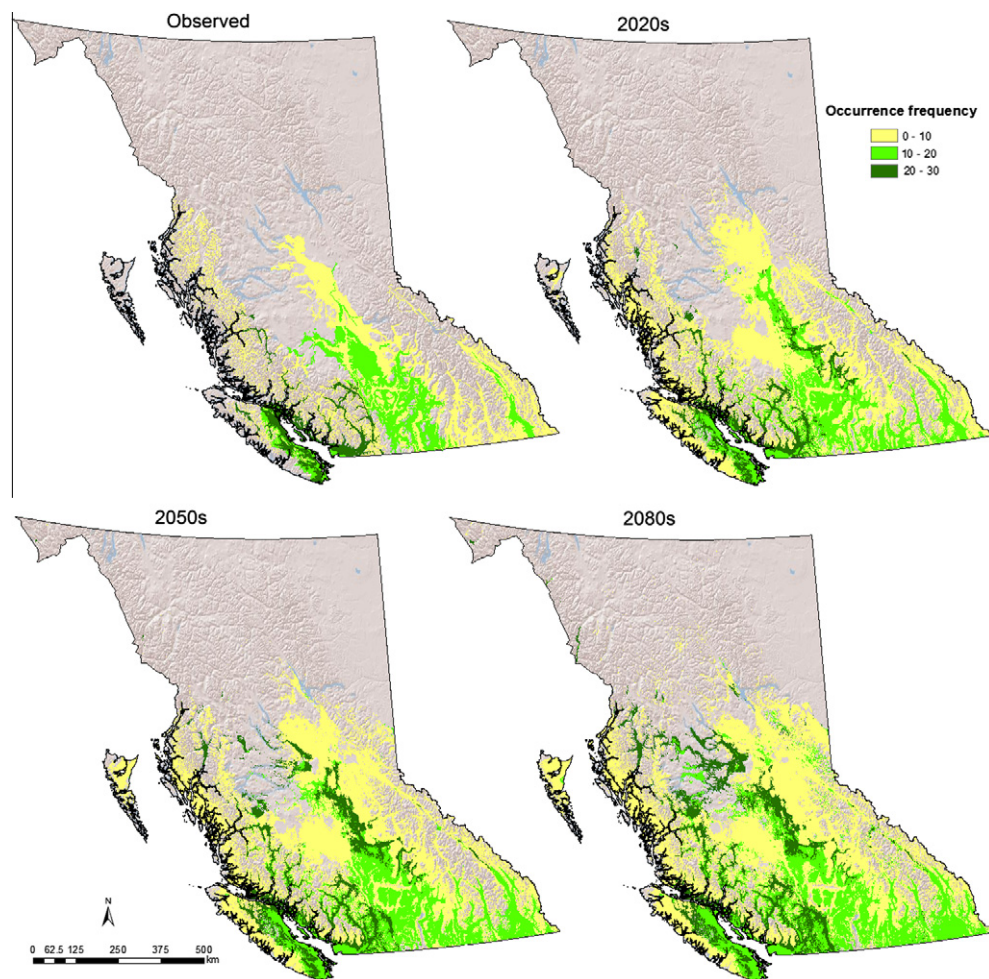
Fig. 9. Random Forest model projections of the geographic distribution of the frequency of occurrence (percent of crown cover) of Douglas-fir (*Pseudotsuga menziesii*) for currently observed, 2020s, 2050s and 2080s. The projections were based on consensus prediction of ecological zone climate habitats and the current extent of Douglas-fir in these zones.

Fig. 10. Number of Douglas-fir seedlings annually planted during 2000–2010 and potentially needed for projected climate envelopes for ecological zones in 2020s, 2050s and 2080s based on consensus projections using 20 climate change scenarios. Zones with the number of seedlings planted or needed less than 0.1 million are not shown in the figures.

While consensus projections illustrated consistent patterns of potential change in distributions of ecosystem climate niches across broad gradients of future temperature and precipitation,

the maps of consensus strength (Fig. 7) together with projections for individual climate change scenarios for 2050 (Fig. 8) provided insight about ecosystem sensitivity and threshold responses to climate change. We found that subalpine boreal Spruce–Willow–Birch (SWB) and Sub-Boreal Spruce (SBS) ecosystems were amongst the most sensitive to climate change. While we projected stable boreal (BWBS) ecosystems of northeastern BC (see discussion above), the virtual disappearance of these other boreal climates is the first large projected change to occur in BC under optimistic climate change scenarios, which incorporate social and economic constraints on GHG emissions and modest mean air temperature increases. The sensitivity of boreal regions to climate change is widely acknowledged, with future ecosystem shifts in western boreal forests expected as climate change increases disturbance severity and reduces boreal tree regeneration success (Hogg and Schwarz, 1997; Soja et al., 2007; Lenton et al., 2008; Gonzalez et al., 2010). Alpine ecosystems are also expected to be highly sensitive to global warming, with only small increases in temperature quickly generating ecosystem changes (Gottfried et al., 1998; Theurillat and Guisan, 2001; Kullman, 2002). While BC alpine ecosystem are quite sensitive to climate change, our projections indicated substantial variation in the sensitivity of BC alpine ecosystems (BAFA, CMA, IMA), a finding that is consistent with other studies conducted across large, subcontinental scales (Lenton et al., 2008). Other substantial BC ecosystem shifts – such as the replacement of subalpine ecosystems by more productive

lower elevation forests and conversions of forests to the pine savanna (PP climate) or grasslands (BG climate) – are most likely under more pessimistic climate change scenarios with larger temperature increases and precipitation changes.

4.3. Uncertainty and management applications

Uncertain future ecosystem distributions pose major challenges for natural resource managers. This uncertainty can be reduced when forecasts are built using powerful statistical modeling techniques (Elith et al., 2008; Lawler et al., 2006; Marmion et al., 2009), including RF. However, uncertainty associated with an array of plausible future climates must be assimilated into management planning. Our consensus maps of the most frequently projected ecosystem climate niches for a wide range of future climates, accompanied by maps of model agreement (Fig. 7A–C), provide resource managers with a measure of certainty about the future distribution of ecosystem climates.

Management may be more straightforward for regions where model consensus is strong and where ecosystems are projected to change little over time (e.g., southern coastal BC; wet mountainous areas of southeastern BC; and the boreal zone of northeastern BC) (Fig. 7). However, in situations where agreement among model projections is low, management will be more complex, requiring flexible policy frameworks that facilitate a varied portfolio of management activities (including some new ones) that capitalize on new climatic environments and reduce the risk of catastrophic socio-economic losses. Spatial variation in management practices applied at stand and landscape levels should be higher in areas with more uncertain futures.

The Douglas-fir case study demonstrated how projected shifts in ecosystem climates could be applied to project changes in the climate envelopes for individual tree species, which in turn could be used to determine where a species could be planted in the future and approximate the number of seedlings needed for planting in future climates. We projected that climate habitat for Douglas-fir would expand substantially in the future as the climate becomes more suitable for this frost-sensitive species at higher elevations and at more northerly latitudes. Our finding agrees with other published projections, although Hamann and Wang (2006) projected a more dramatic expansion of Douglas-fir habitat in BC as northeastern boreal ecosystem climates transitioned to climates for Interior Douglas-Fir ecosystems. While Rehfeldt et al. (2006) projected increases in Douglas-fir habitat in the western United States until 2060, and then a slight decrease for 2090, McKenney et al. (2007) projected an increase when the entire species range was considered. Expansion of suitable Douglas-fir climates in BC suggests it would be appropriate to reforest logged sites with this species over a much larger geographic area than in the past, and planning to expand seed source inventories and seed orchard capacity to facilitate increased planting over larger areas could begin now, if the ecological risks of species range expansion are deemed sufficiently low and there is social acceptance of this expansion on public lands. Our consensus-projection-based estimation of seedlings needed for the future periods provides a reasonable guess to start with for planning considering multiple climate scenarios.

While our RF model more accurately predicts the geographic distribution of BC ecosystem climate niches than the previous model (Hamann and Wang, 2006), it does not yet account for the possibility that novel climate niches will develop as the global climate continues to change. As mentioned above, Mbogga et al. (2010) and Rehfeldt et al. (2012) projected the expansion of dry grassland and steppe forest climates from south-central Alberta and central United States into northeastern BC. Climate adaptation strategies in these novel BC climates could be similar to the guid-

ance already provided for managing these ecosystems in Alberta. Rehfeldt et al. (2012) also project the development of climates in southeastern BC that are novel to all of North America. In these situations, like those where projections about future climate niches are highly uncertain, management to adapt to climate change will be more complex, requiring a varied portfolio of activities that spread the risk of management failures.

This study demonstrates that climate envelope models built with RF provide a more accurate basis for projecting the potential effects of climate change on BC ecosystems than previously used statistical approaches. It also shows how mapped consensus projections can incorporate uncertainty about future climate into the development of climate change adaptation strategies. We emphasize that these climate change models do not necessarily project the future distribution of ecosystems or their constituent species. Within ecosystem climate niches, local topography (e.g., aspect and slope) or specific site conditions (e.g., soil texture) may modify climate impacts on the distribution of species and species assemblages. Until climate envelope models are better able to incorporate these local effects into projections, or they can be integrated with mechanistic models implemented over smaller spatial scales, we will continue to rely on local expertise to appropriately implement the results of ecosystem climate niche models.

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