POTENTIAL EFFECTS OF CLIMATE CHANGE ON ECOSYSTEM AND TREE SPECIES DISTRIBUTION IN BRITISH COLUMBIA

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Abstract. A new ecosystem-based climate envelope modeling approach was applied to assess potential climate change impacts on forest communities and tree species. Four orthogonal canonical discriminant functions were used to describe the realized climate space for British Columbia's ecosystems and to model portions of the realized niche space for tree species under current and predicted future climates. This conceptually simple model is capable of predicting species ranges at high spatial resolutions far beyond the study area, including outlying populations and southern range limits for many species. We analyzed how the realized climate space of current ecosystems changes in extent, elevation, and spatial distribution under climate change scenarios and evaluated the implications for potential tree species habitat. Tree species with their northern range limit in British Columbia gain potential habitat at a pace of at least 100 km per decade, common hardwoods appear to be generally unaffected by climate change, and some of the most important conifer species in British Columbia are expected to lose a large portion of their suitable habitat. The extent of spatial redistribution of realized climate space for ecosystems is considerable, with currently important sub-boreal and montane climate regions rapidly disappearing. Local predictions of changes to tree species frequencies were generated as a basis for systematic surveys of biological response to climate change.

Key words: bioclimatic analysis; British Columbia; climate change; climate envelope; predictive vegetation mapping; spatial predictions; species distributions and ranges.

INTRODUCTION

A growing number of studies suggests that global climate warming affects a wide range of species and ecosystems (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). Biological response is particularly prevalent in the northern sub-boreal, boreal, and subarctic ecosystems where the warming signal is strongest (Zhou et al. 2001, Bogaert et al. 2002, Lloyd et al. 2002, Lloyd and Fastie 2003). Over the past decade, British Columbia (49°-60° latitude) has experienced a warming trend that approximately matches climate change predictions from general circulation models published in the mid 1990s (Johns et al. 1997, Mote 2003). This relatively small increase in mean annual temperature, ~0.7°C for British Columbia, already appears to have had remarkable economic and ecological impacts. The current mountain pine beetle epidemic is the largest documented for this species, spreading over 4.1×10^6 ha (Ebata 2004). This outbreak may be partially caused by lack of low winter minimum temperatures, which would normally reduce the popu-

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lations of this native-insect pest by killing the larvae, and by the beetle's temperature-controlled development cycles and lack of diapause (Logan and Powell 2001, Powell et al. 2000, Carroll et al. 2004). A minor native disease, Dothistroma needle blight, which is starting to cause widespread damage in northeast British Columbia, has been causally linked to increased frequency of warm and moist conditions that were experimentally found to be favorable for infections by this fungus (Woods et al. 2005). In southern and interior British Columbia, substantial reforestation failures and high frequency of wildfires were attributed to drought in combination with record temperatures, particularly in 1998 and 2003 (Filmon 2004). Natural variability in climate and nonclimatic factors may play a role in these incidents: nevertheless, the current problems raise the question of whether a continued warming trend, predicted to show an increase of $\sim 0.5^{\circ}$ C per decade, could threaten British Columbia's ecosystems and forest resources.

One way to address this issue is through bioclimate envelope studies, which use climate data as independent predictor variables and biological data as dependent variables to generate a predictive model for species or ecosystem distributions. Climate change predictions overlaid on interpolated baseline climate data are then used to generate maps of current and future species distributions, which can be evaluated with geographical

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information systems. Such studies generally show that temperate tree species will expand their range northward and into higher elevations and that they will lose suitable habitat at the southern end of their original distribution (Talkkari and Hypen 1996, Iverson and Prasad 1998, 2001, 2002, Iverson et al. 1999). It is widely understood that shifts in vegetation zones are not entirely determined by shifts in climate. It has been shown that soil, local topography, groundwater level, and other factors may influence plant species distributions (Talkkari and Hypen 1996, Iverson and Prasad 1998). Furthermore, under climate change the interactions between climate variables and those additional factors might become relevant (Ferguson and George 2003). Also, elevated atmospheric CO₂ levels could significantly increase growth rates of species under drought stress, although the effect might be negligible otherwise (Knapp and Soule 1996, Idso 1999, Saxe et al. 2001, Polley et al. 2003). In addition, different tree species or populations may have different potentials to respond to climate change through plasticity and genetic adaptation (Rehfeldt et al. 1999, 2001, 2002). Species also have different capabilities of migrating through complex landscapes to favorable habitats (Schwartz et al. 2001, Nathan et al. 2002). Finally, the realized niche of a species on a landscape unit is determined through competitive exclusion, integrating all of the above-mentioned factors and their interactions (Loehle and LeBlanc 1996, Loehle 2003, Schmitz et al. 2003).

It is obviously impossible and also not necessary to consider all of these processes when modeling the impacts of climate change on a large geographic scale. Climate envelope models can be instructive, not by predicting changes literally, but by quantifying differences among current distributions and potential habitats under potential climate change scenarios (Pearson and Dawson 2003). Also, despite the shortcomings of climate envelope models, the general patterns of predicted species range shifts often match observed biological trends (Parmesan et al. 2005). Climate envelope modeling can also be useful in another, more practical way. For ecosystem restoration, conservation planning, plantation forestry, or genetic resource management many fundamental limitations of bioclimate envelope studies do not apply. Natural resource managers are free to match species and genotypes to environments for which they are optimally adapted and can facilitate seedling survival, control competition, and direct successional processes with various management techniques. Bioclimate envelope modeling is well suited to assisting these programs in matching management objectives for specific sites with anticipated future climates or observed climate change trends for these locations.

Techniques that have been employed for bioclimate envelope modeling include generalized linear models (Bakkenes et al. 2002), generalized additive models (Frescino et al. 2001), regression tree analysis (Iverson and Prasad 1998, Thuiller et al. 2003*b*), and artificial neural networks (Berry et al. 2002, Pearson et al. 2002). Different models sometimes result in different predictions, and individual species may show an optimummodel fit using any of these models (Moisen and Frescino 2002, Thuiller et al. 2003a). Some experts have suggested evaluating several models for each species and choosing the best method for making predictions (Thuiller 2003). In this study, we present a different approach. We explore whether relatively straightforward modeling methods at the ecosystem level rather than the species level can result in accurate predictions of species habitat. For this purpose, we use the Biogeoclimatic Ecological Classification (BEC) system (Ministry of Forests and Range, British Columbia, Canada, available online),² which hierarchically delineates major forest types, plant communities, and climatic variants of these communities. BEC system maps at a scale of 1:250 000 are widely used as a common framework for natural resource management and ecological research (Meidinger et al. 1991). The three main objectives of this paper are (1) to determine the ability of climate variables to distinguish plant communities and delineate the realized environment of ecosystems; (2) to analyze how the realized climate space of current ecosystems changes in extent, elevation, and spatial distribution under climate change scenarios; and (3) to evaluate the implications for potential tree species habitat. In addition, we make predictions of changes to tree species frequencies for each ecosystem as a basis for systematic surveys of biological response to climate change. Community-wide predictions in combination with systematic field assessments could provide a powerful tool to test the hypothesis that observed biological trends are causally related to climate change.

Methods

Baseline climate data

Our baseline climate data are derived from commercially available coverages that were generated using the Parameter Regression of Independent Slopes Model (PRISM; available online)³ (Oregon Climate Service, Oregon State University, Corvalis, Oregon, USA) to interpolate climate normal data observed at weather stations for the period 1961-1990 (Daly et al. 2000, 2002). While this methodology is generally considered "state of the art" for generating baseline climate data, we find that available data sets at \sim 2- and 4-km resolution are not sufficient for mountainous environments such as British Columbia. Because PRISM climate estimates are based on a considerably smoothed elevation surface, the inferred climatic envelopes for species or ecosystems are too narrow, leading to overestimates of climate change impacts and possibly to false inferences that predicted future climates have no

² (http://www.for.gov.bc.ca/hre/becweb/)

³ (http://www.ocs.oregonstate.edu/prism/contacts.phtml)

analogue to current climates (Hamann and Wang 2005). To overcome this problem we developed simple elevation adjustment formulas that allow "intelligent" downscaling of the PRISM model using high-resolution digital elevation models (Hamann and Wang 2005, Wang et al. 2006). For this study, we generated a 400-m resolution climate data set in the British Columbia Albers Equal Area Conic projection (information available online),⁴ covering the study area with ~ 6 million tiles. Starting with 36 monthly variables (climate normal measurements of mean minimum temperature, mean maximum temperature, and precipitation as defined by the World Meteorological Organization) we calculated or estimated 15 biologically relevant and interpretable variables for this study, including various degree-days, frost-free period, dryness indices, temperature extremes, and snowfall according to Wang et al. (2006). Spatial coverages of 75 monthly, seasonal, annual, and derived climate variables are publicly available through British Columbia's Ministry of Forests and Range data warehouse (available online).⁵

Climate change data

Most statistics in this study are based on an ensemble simulation of the older general circulation model CGCM1gax of the Canadian Centre for Climate Modeling and Analysis (Flato et al. 2000), which implements the IS92a emission scenario for the 30-year periods ca. 2025, 2055, and 2085 (IPCC 2001). Predictions of precipitation and temperature variables for British Columbia from this model are "middle of the road" values compared to other implementations of the IS92a scenario. The Intergovernmental Panel on Climate Change (IPCC 2001) recommends using a variety of other models to obtain a range of predictions reflecting uncertainty arising from forecasting CO₂ emissions and general circulation model implementations. We also evaluate two newer scenarios, the more optimistic SRES B2 "stewardship" emission scenario and the more pessimistic A2 "enterprise" emission scenario implemented through the general circulation models CGCM2 and HadCM3 and available through the Canadian Institute of Climate Studies (CICS 2004). An even greater magnitude of uncertainty than from alternate emission scenarios arises from the discrepancies among very coarse-scale predictions of directional climate change by GCMs and the observed local changes due to new weather patterns in a complex landscape such as British Columbia. We therefore also applied stronger, systematic changes to groups of related climate variables in order to explore the sensitivity of model predictions to changes that might locally be more pronounced than predicted by any GCM, particularly in precipitation. All predictions of climate change generated by GCMs were expressed as anomalies (deviations from the 1961–1990 normals). In order to add them to high-resolution baseline data without artifacts at GCM tile boundaries, anomalies were interpolated to the same 400-m resolution data using Anusplin software (Hutchinson 2005).

Ecosystem delineation

The Biogeoclimatic Ecological Classification (BEC) system is a hierarchical classification system that subdivides the land base of British Columbia into 14 zones, 97 subzones, and 152 variants (Pojar et al. 1987, Meidinger et al. 1991). Subzones are the basic unit of this system, representing plant communities that were defined using a Braun-Blanquet type approach (Krajina 1959, 1976, Klinka et al. 1991). Ecosystems were then spatially mapped using empirical rules based on latitude, longitude, elevation, slope, and aspect (Eng and Meidinger 1999). The finer division of BEC subzones into BEC variants accounts for climatic differences within subzones that are not distinctly reflected in plant community composition. BEC zones, the higher hierarchical division, represent major forest types, each having a homogeneous macroclimate. Predictions of ecosystems based on climate data were carried out at the BEC variant level, and all results are summarized or displayed at the BEC zone level for clarity and concise reporting. We used version four of this coverage, available online through the Ministry of Sustainable Resource Management of British Columbia (MSRM 2002). The coverage was rasterized at a 400-m resolution according to the BEC variant present at the tile center.

Predictions of ecosystems based on climate data require the landscape to be subdivided into relatively homogeneous (with regard to climate) spatial units that should span only a limited elevation range (not more than a few hundred meters). The BEC variants used in this study typically cover $0.5-1 \times 10^6$ ha. A few variants of the interior plateau and the prairies are much larger, and some submontane variants (around mountain tops) are much smaller as well as highly discontinuous. Only the Alpine Tundra zone of this ecosystem delineation did not meet the requirements for this analysis, representing all areas above tree line throughout British Columbia. We therefore subdivided the Alpine Tundra zone according to the following mountain ranges: South Coast, Mid Coast, North Coast, Northern Rocky Mountains, Southern Rocky Mountains, Central Interior (leeward side of South Coast and Mid Coast), Columbia, and Cassiar. Each of these "subzones" was then divided into "variants" by division into two elevation bands at the point where permanent glaciers typically form in each subzone if the topography is suitable.

Bioclimate envelope modeling

For identification of relevant climate variables, we used canonical discriminant analysis (Hand 1981),

⁴ (http://srmwww.gov.bc.ca/gis/bceprojection.html)

⁵ (http://www.genetics.forestry.ubc.ca/cfgc/ climate-models.html)

implemented through PROC CANDISC and PROC DISCRIM of the SAS Statistical Software Package (SAS Institute 2001). As opposed to principal component analysis, which maximizes the variance explained among all observations, discriminant analysis maximizes the variance between groups (BEC variants), and therefore indicates which of the original variables differentiate ecosystems best. First, we used weather station data to test which climate variables meet statistical assumptions for discriminant analysis (univariate normality and homogeneity of covariance matrices among groups; we omitted tests of multivariate normality). This is not possible with interpolated climate coverages, because the statistical power of the tests is inflated by using a very large number of highly autocorrelated observations. Also, the tests of assumptions were not strictly necessary because we were only interested in the capability of PROC DISCRIM to assign observations to groups, and we did not use any inferential statistics in this study. However, satisfying these assumptions is generally beneficial because doing so minimizes misclassification error rates. As a result, precipitation variables and heat-moisture indices were log₁₀-transformed for all subsequent analysis.

Next, we used interpolated climate data to develop four discriminant functions with PROC CANDISC and used these functions instead of the original climate variables as input for PROC DISCRIM to avoid overparameterization. (This step is a precaution and did not prove necessary in this case.) PROC DISCRIM assigns individual observations (tiles of multivariate climate data) to groups (BEC variants), according to the Mahalanobis distance between an observation and the mean vector of the closest group, which may not necessarily be the original BEC variant. The classification procedure was repeated after climate change scenarios were applied. If the Mahalanobis distance exceeds the distance observed among a group mean vector and its original members, PROC DISCRIM still carries out the classification. Therefore, we recalculated the Mahalanobis distance between the observation and the mean vector of the assigned group using the algorithm 7.2.2. in Falk et al. (1995) implemented through PROC IML. If the maximum distance to its original members was exceeded, the observation was marked as not matching any current climatic conditions in British Columbia. The percentage of correct allocations and the misclassification error among groups was subsequently summarized with PROC UNIVARIATE at the BEC zone level because the matrices would be too large to be informative at the variant level. Similarly, all changes from a current BEC variant to a predicted BEC variant after climate change were summarized at the BEC zone level.

Maps of potential habitat for tree species

Maps of species distribution and frequencies were generated by simply replacing current and predicted BEC variants with known species frequencies for these variants (Hamann et al. 2005). These species frequencies were obtained by overlaying the BEC system coverage with a database of 34 000 botanical inventory plots, each 0.4 ha in area. This database contained a measure of percentage ground cover for each species for several vegetation layers, and we used this measure to calculate an expected percentage ground cover for each species in each BEC variant (Hamann et al. 2005). Unlike distribution maps that delineate actual forest stands and include changes due to human disturbance, our range maps delineate the potential habitat of a species with frequencies expected under a natural disturbance regime. Predicted changes in species frequencies were summarized by BEC zone with PROC UNIVARIATE evaluating a from-to matrix of BEC variant changes after applying climate change scenarios.

RESULTS AND DISCUSSION

Relevance of climate variables

Four orthogonal canonical discriminant functions are required to account for most of the variance in climate variables among ecosystems in British Columbia. These independent climate dimensions account for 90% and 92% of the total variance in weather station data and interpolated climate coverages, respectively. Virtually identical discriminant functions were obtained for weather stations and interpolated climate coverages, indicating that the analysis works properly with autocorrelated data, as well. The linear combinations are plotted in Fig. 1 (upper left, weather station data; lower left, interpolated data) and the correlations among the canonical functions and the original climate variables are given in Table 1. The first canonical discriminant function for interpolated data (eigenvalue = 9.8, variance explained = 0.56) reflects a gradient from maritime to continental climate with milder winters and more precipitation on the coast due to a strong oceanic influence (Fig. 1, Map CAN1, where tiles of interpolated climate data are colored according to the discriminant function score. The second, independent canonical discriminant function (eigenvalue = 4.9, variance explained = 0.23) mainly reflects a temperature gradient and shows particularly high correlations with temperature variables measured during the growing season such as degree-days and summer temperature (Table 1). This climate dimension, independent from the first, can be observed along elevational gradients (Fig. 1, Map CAN2). The third and fourth discriminant functions with eigenvalues >1 explain 9% and 4%, respectively, of the variance and are significant at levels of P < 0.05. The third and fourth functions are important to reliably separate some interior BEC variants. All other canonical discriminant functions can be dropped without affecting the predictions or misclassification error rates.

It is generally assumed that the choice of climate variables is an important decision for bioclimate envelope modeling. Parmesan et al. (2000) points out



FIG. 1. Canonical discriminant analysis of weather station data (top) and PRISM data (bottom) for Biogeoclimatic Ecological Classification (BEC) zones. Positive scores in CAN1 indicate continental conditions; negative scores indicate maritime conditions. Positive scores in CAN2 indicate cold/wet climate; negative scores indicate warm/dry climate. For complete names of BEC zones, refer to Fig. 2.

that extreme climatic events are responsible for ecological responses to general climatic trends, and that such climate variables should therefore be included in this type of analysis. However, average measurements, such as growing degree-days or mean annual temperature, may be effective drivers of species ranges. These variables do not directly "kill" individuals (as would extreme cold or extreme drought), but under certain average conditions, give a competitive advantage to individuals, populations, or species with maximum fitness. While this type of analysis provides some indication of what climate variables are relevant to distinguish ecosystems (and by implication relevant to determine species ranges in general), it should be noted

			Weather s	tation data	a		Interpola	ated data	
Climate normal	Code	CAN1	CAN2	CAN3	CAN4	CAN1	CAN2	CAN3	CAN4
Mean annual temperature	MAT	-0.72	0.54	-0.38	-0.07	-0.55	0.82	-0.01	0.00
Mean coldest month temperature	MCMT	-0.88	0.39	-0.12	-0.16	-0.82	0.47	-0.06	0.01
Extreme minimum temperature	MIN	-0.90	0.14	-0.17	-0.15	-0.92	0.45	-0.05	-0.17
Mean warmest month temperature	MWMT	-0.01	0.66	-0.54	0.02	0.07	0.88	-0.24	-0.05
Extreme maximum temperature	MAX	0.24	0.55	-0.28	0.06				
Continentality†	CONT	0.93	-0.16	-0.08	0.18	0.90	-0.05	-0.17	-0.13
Mean annual precipitation (ln)	MAP	-0.86	-0.20	0.30	0.29	-0.89	-0.23	0.40	-0.19
Mean summer precipitation (ln)	MSP	-0.48	-0.32	0.43	0.57	-0.66	-0.40	0.41	0.51
Mean winter precipitation (ln)	MWP	-0.91	-0.12	0.28	0.20	-0.90	-0.17	0.29	0.12
Precipitation as snow (ln)	PAS	0.45	-0.12	0.69	0.27	-0.41	-0.63	0.61	0.27
Annual heat moisture index (ln):	AHM	0.68	0.43	-0.45	-0.31	0.68	0.62	-0.44	-0.15
Summer heat moisture index (ln)§	SHM	0.40	0.46	-0.53	-0.46	0.58	0.66	-0.42	0.49
Number of frost-free days	NFFD	-0.86	0.59	-0.39	-0.05	-0.60	0.70	-0.39	-0.05
Degree-days >5°C	DD5	-0.40	0.54	-0.56	-0.08	-0.15	0.90	-0.53	-0.12
Degree-days <0°C	DD0	0.90	-0.14	0.25	0.15	0.82	-0.63	0.32	0.14

TABLE 1. Loadings of canonical discriminant functions with weather station data and interpolated data.

Note: Log-transformed climate variables are designated as (ln); boldface indicates the most important variables.

† MWMŤ – MCMT.

 $\frac{1}{2}$ (MAT + 10)/(MAP × 1000).

 $\frac{1}{8}$ (MWMT)/(MSP × 1000).

that many climate variables are highly correlated (Table 2). To an even greater degree, this correlation applies to monthly and seasonal averages (data not shown), making it impossible to determine the variable that is the actual driver of biological response, as pointed out by Parmesan et al. (2005). In fact, we can randomly drop up to 10 of the 15 variables used in that analysis, and the canonical discriminant analysis still "forces" any set of remaining variables into composites virtually identical to CAN1 and CAN2, shown in Fig. 1.

We interpret these results as a good illustration that bioclimate envelope studies can only assist in determining which factors limit the extent of an ecosystem or a species range. We can reliably extract composite variables that represent relevant variables, but the mechanistic drivers of changes to ecosystem and species distribution remain unknown and have to be determined through experimental studies or empirical observations (Parmesan et al. 2005). For climate change modeling, this is unproblematic as long as correlations among measured variables and the unknown mechanistic drivers remain constant under future scenarios. It has been suggested that the frequency of extreme events may increase disproportionately compared to changes in average variables (Schaer et al. 2004). However, we find no indication that the correlation matrix of climate variables for British Columbia (Table 2) changes when GCM predictions are added to baseline data (data not shown), and currently we have no quantitative basis for modeling under a different assumption.

Model fit and model limitations

Misclassification error rates in this analysis are defined by the multivariate technique that we used, although other measures are available to evaluate the predictive capability of ecosystem-based (or biomebased) climate envelope models (Sykes et al. 1999). Misclassification error rates range from 10% for

TABLE 2. Correlation coefficients for 15 biologically relevant climate normals (1961–1990) measured at 440 weather stations in British Columbia, Canada.

Climate variable	Code	MCMT	MIN	MWMT	MAX	CONT	MAP	MSP	MWP	PAS
Mean annual temperature	MAT	0.93	0.82	0.66	0.27	-0.73	0.40	0.01	0.48	-0.68
Mean coldest month temperature	MCMT		0.92	0.36	0.00	-0.93	0.61	0.21	0.68	-0.62
Extreme minimum temperature	MIN			0.23	-0.19	-0.89	0.68	0.31	0.74	-0.58
Mean warmest month temperature	MWMT				0.72	0.01	-0.23	-0.41	-0.16	-0.36
Extreme maximum temperature	MAX					0.28	-0.35	-0.43	-0.30	-0.01
Continentality	CONT						-0.74	-0.38	-0.79	0.52
Mean annual precipitation (log)	MAP							0.82	0.99	-0.06
Mean summer precipitation (log)	MSP								0.73	0.20
Mean winter precipitation (log)	MWP									-0.12
Precipitation as snow (log)	PAS									
Annual heat moisture index (log)	AHM									
Summer heat moisture index (log)	SHM									
Number of frost-free days	NFFD									
Degree-days $>5^{\circ}C$	DD5									
Degree-days <0°C	DD0									

Note: Log₁₀-transformed climate variables are designated as (log); boldface indicates correlation coefficients >0.90).

ecosystems in areas of low topographic relief to 60% for ecosystems that occupy narrow elevation bands in steep mountains (Appendix A: Table 1). Even large misclassification errors occur only among immediately adjacent zones and on a very small spatial scale resulting in an apparently almost-perfect match when visualized on a map (Appendix A: Fig. A1). Note that an independent model test, e.g., randomly subdividing the data set for model development and model testing is not possible in our case, because neither interpolated climate data nor rasterized BEC variants are independent samples. The misclassification error rates remain identical even if we use a random 1% subset of the data (60000 observations) to develop a model and then predict the remaining 99%. To save computing time we build models using a systematically subsampled data set containing 6.25% of the tiles. Because the BEC delineation is spatially explicit at a map scale of 1:250 000 we had to work at ~ 100 to 1000 times higher spatial resolution than most other bioclimate envelope-type studies in order to obtain reasonably low misclassification error rates. When working at lower resolutions, for example the PRISM data native 1.25 arcmin resolution, misclassification was very high (Appendix A2: Fig. A1). Also, BEC zones were classified into narrower climatic envelopes because PRISM predictions are based on a considerably smoothed elevation surface, which leads to overestimating the effect of climate change (Hamann and Wang 2005).

Because we had no independent statistical test to evaluate the model and explore its limitations, we used a different assessment. A good indication of the model's suitability to predict ecosystem and species distributions under climate-warming scenarios should be its capability of predicting ecological zones and implied species distributions south of British Columbia, extrapolating into warmer climatic conditions (Appendix A: Fig. A2). We compared these extrapolations visually using Little's (1971) approximate species range maps (Appendix A: Figs. A3–7). If the prediction for an ecosystem in these

TABLE 2. Extended.

AHM	SHM	NFFD	DD5	DD0
-0.07	0.18	0.91	0.90	-0.85
-0.33	-0.07	0.92	0.69	-0.94
-0.46	-0.20	0.92	0.58	-0.93
0.48	0.63	0.39	0.89	-0.23
0.48	0.57	-0.04	0.51	0.14
0.54	0.33	-0.83	-0.38	0.91
-0.94	-0.76	0.59	0.08	-0.65
-0.88	-0.97	0.22	-0.24	-0.25
-0.90	-0.66	0.65	0.16	-0.71
-0.16	-0.28	-0.72	-0.64	0.72
	0.89	-0.33	0.22	0.41
		-0.08	0.45	0.15
			0.74	-0.95
				-0.61

maps is dotted, it means that it has been marked as having no exact match to current ecosystems in British Columbia. For example, orange dots in California (Appendix A: Fig. 2) indicate that no similar climatic conditions are observed in British Columbia, and no ecosystem can be properly matched to what, in fact, is an oak savannah; however, the ecosystem that is climatically most similar is coastal Douglas-fir (CDF, orange). Because Douglas-fir (*Pseudotsuga menziesii*) is present in the CDF ecosystem, the model will predict the presence of the species for this area in California, but it extrapolates beyond data coverage (indicated by a dotted distribution).

We examined a number of representative species distributions, starting with a common interior species, *Pinus contorta*. Extrapolations to the south appear to be mostly correct, including the prediction of two small, outlying populations as far away as southern California (Appendix A: Fig. A3). That is possible because climatic conditions equivalent to southern desert conditions can be found in British Columbia, resulting in a more or less complete bracketing of the species' southern climatic limits within British Columbia. On the other hand, our extrapolations overpredicted the species range in the north and the Prairies, which could be due to (1) lack of data to accurately model northern range limits; (2) factors other than climate, e.g., soils, that limit the species distribution in the prairies; (3) the species still being in the process of expanding north into correctly predicted habitat. It is likely that the last explanation applies to Pinus contorta in that example (Cwynar and Macdonald 1987). However, for climatically more homogeneous regions, such as the Canadian prairies or the Great Plains in the United States, we expect that additional factors have to be included to accurately model species distributions. Next, we investigated an example for a common coastal species Alnus rubra (Appendix A: Fig. A4). Small, outlying populations in Idaho are correctly predicted, but the model fails to appropriately delineate the southern coastal range limit in California. In that case we had a clear example of lack of equivalent climate in British Columbia (indicated by the dotted areas) to accurately model the species' southern range limit. Pseudotsuga menziesii (Appendix A: Fig. A5) serves as an example for a species that has only about half of its range inside British Columbia. It has both a coastal and interior distribution, and similar limitations as discussed for the two examples above apply for extrapolations beyond British Columbia (overprediction for the Great Plains and inability to simulate the southern coastal range limit). Observations described in the previous examples apply to two more examples for species that occur infrequently in British Columbia, Larix occidentalis in the interior and Arbutus menziesii on the coast (Appendix A: Figs. A6 and 7). At least for high-elevation species where we only had data from the northern edge of the distribution, we could predict reasonably well the southern range limit, presumably because of equivalent low-elevation range boundaries that can be observed in British Columbia. On the other hand, predictions of coastal distributions are marked as unreliable for Washington (although they are usually correctly predicted), and the model always fails to correctly predict southern range limits of coastal species in California. These limitations do not seem to be of concern because climate predicted by GCMs for British Columbia do not approach conditions equivalent to those observed in California, where a large portion of the species covered in this study have their southern range limits.

We find it astonishing that many unexpected and apparently random features of species distributions can be predicted using climate variables alone and by extrapolating far beyond the area sampled. To give another example, Alnus tenuifolia (not shown) has an entirely interior distribution except for a small coastal population in the northern corner of the Alaska Panhandle. That is correctly predicted without any data from this region. The model appears to support the view that climate is the primary factor controlling the distribution of plants (Tuhkanen 1980, Woodward 1987, Woodward and Williams 1987). At least in landscapes with strong climatic gradients, such as the Pacific Northwest, distributions for many species can be quite accurately modeled without other environmental parameters, provided that high-resolution climate data and accurate species frequency maps or ecosystem maps are available.

Effect of climate change on ecosystem distribution

Fig. 2 and Table 3 summarize how the climatic envelope of current ecosystems would shift according to the general circulation model CCGA1gax of the Canadian Centre for Climate Modelling and Analysis (additional statistics, results from other models, and high-resolution regional maps are available in Appendix B). Many zones that are partially or entirely in mountainous areas shift upward (AT, CWH, ICH, SWB, and MH). The Mountain Hemlock zone, which consists of a narrow band on the east side of the coast mountains, appears to be particularly vulnerable. By 2055 there is almost no spatial overlap with the zone's current climatic envelope (Table 3, Appendix B: Table B2 and Fig. B1). A notable exception to this pattern of upward elevation shifts is the climatic envelope of the Montane Spruce (MS) ecosystem, which only shows minor changes in average elevation but is largely reduced in extent by its changing to IDF and SBS climates (Table 3, Appendix B: Fig. B1). The largest shifts of climatic envelopes toward the north can be observed in ESSF, PP, and IDF zones (Table 3). The north shift statistics in Table 3 for AT and MS have to be interpreted in conjunction with the maps (Fig. 2). Since the measurements represent average locations of ecosystems modeled only within British Columbia, the shift also reflects whether a climate region disappears

more rapidly in the north or in the south. The largest absolute area changes are the initial expansion of the climatic envelope for Interior Cedar Hemlock (ICH) and the rapid reduction of the Alpine Tundra (AT) and Spruce–Willow–Birch (SWB) climates by 2025. Subsequently, Interior Douglas-fir (IDF) and Ponderosa Pine (PP) climate regions expand throughout the interior plateau, replacing current climate envelopes of subboreal and boreal ecosystems (SBS, SBPS, and BWBS).

In this analysis, we do find climate regions under climate change scenarios that today have no equivalent in British Columbia. However, they are restricted to small areas within the predicted Coastal Douglas-fir (CDF) and Bunchgrass (BG) zones and have not been treated separately. Equivalent ecosystems that fit the descriptions of those zones exist farther south in the United States. The shift of the realized climate space may be approximately visualized by shifting the coordinate system of plots in Fig. 1 down (towards warmer temperatures) and slightly left (toward less continental conditions). Only the warmest and driest ecosystems plotted at the bottom of the graph (CDF and BG) lack equivalents today. That also applies in theory to the bottom fringe (warmest areas) of the transition zone between coastal (left) and interior ecosystems (right). However, those transition zones occur only in valleys that cross the coast mountains into the interior. The zones have almost no spatial representation in the actual landscape and are usually not mapped. (Note the open scatter of relatively few tiles where CAN1 = -2 to 0 between the solid blocks representing the coastal and interior ecosystems in Fig. 1, bottom plot.) The situation may be different for climatically more uniform landscapes, where the realized climate space may be small relative to predicted or past climate change. In that case, climate change might lead predominantly to new realized climate space that has no current equivalent, as described by Jackson and Overpeck (2000).

Similar are the effects of climate change on the climatic envelope of ecosystems in British Columbia according to two other emission scenarios and a different implementation of these scenarios by the Hadley Centre (Appendix B: Fig. B3), simply reflecting slightly different predicted rates of warming. The climate change predictions of the IS92a scenario and the CGCM1 implementation are virtually identical to the newer SRES A2 scenario and the CGCM2 implementation. The more optimistic SRES B2 scenario results in a slightly reduced rate of change and the HadCM3 implementation of the SRES A2 scenario predicts more warming and slightly less precipitation, resulting in accelerated zone shifts. In order to better understand the model's sensitivity to changes in precipitation variables, we applied a series of arbitrary changes to all variables. A uniform 2°C increase to all temperature variables has an effect similar to general circulation model predictions of the same magnitude and appears to be the main driver of zone shifts





FIG. 2. Shift of the climatic envelope of ecological zones based on the ensemble simulation CGCM1gax for the normal periods 2011–2040 (2025), 2041–2070 (2055), and 2071–2100 (2085). The ecological zones are: CDF, Coastal Douglas-fir; CWH, Coastal Western Hemlock; BG, Bunchgrass; PP, Ponderosa Pine; IDF, Interior Douglas-fir; ICH, Interior Cedar–Hemlock; SBPS, Subboreal Pine and Spruce; SBS, Sub-boreal Spruce; BWBS, Boreal White and Back Spruce; MH, Mountain Hemlock; ESSF, Engelmann Spruce–Subapline Fir; MS, Montane Spruce; SWB, Spruce–Willow–Birch; AT, Alpine Tundra.

(Appendix B: Fig. B3). An additional precipitation increase or decrease by 10, 25, 50, and 100% (more than predicted by GCMs) can slow or reverse the anticipated expansion of grassland habitat and dry interior ecosystems (Appendix B: Fig. B3). Although these values are far beyond expectations from GCMs, they may approximate the effect of increased water use efficiency due to elevated atmospheric CO_2 concentration if water is a limiting factor for growth and survival (Knapp and Soule 1996, Idso 1999, Saxe et al. 2001, Polley et al. 2003). As expected, there is no effect from increased or decreased precipitation for wet coastal ecosystems or the moist inland mountain ranges.

Tree species distribution and frequencies

Table 4 provides statistics for changes in distribution and frequency of all tree species in British Columbia (a

		Elev	Elevation shift (m)			rth shift ((km)	Are	a change	(%)
Ecological zone	Code	2025	2055	2085	2025	2055	2085	2025	2055	2085
Alpine Tundra	AT	+168	+303	+542	-5	-67	-210	-60	-85	-97
Bunchgrass	BG	+104	+179	+243	14	16	9	159	418	773
Boreal White and Blue Spruce	BWBS	+37	+56	+199	18	53	78	4	-11	-44
Coastal Douglas-fir	CDF	+0	+4	+7	23	87	156	62	176	336
Coastal Western Hemlock	CWH	+134	+224	+317	30	44	56	27	40	50
Engelmann Spruce-Subalpine Fir	ESSF	+86	+143	+225	154	224	287	6	3	-27
Interior Cedar Hemlock	ICH	+113	+194	+307	72	94	105	112	154	207
Interior Douglas-fir	IDF	+40	-42	+55	85	264	349	38	160	149
Mountain Hemlock	MH	+263	+418	+597	35	69	109	-24	-52	-79
Montane Spruce	MS	-28	-22	+85	149	302	446	-19	-40	-68
Ponderosa Pine	PP	+175	+186	+218	10	278	614	12	53	452
Sub-boreal–Boreal Pine and Spruce	SBPS	+143	+282	+471	-15	-13	-11	-49	-82	-98
Sub-boreal–Boreal Spruce	SBS	+44	+191	+384	40	198	126	-13	-69	-85
Spruce–Willow–Birch	SWB	+179	+410	+516	63	53	38	-69	-93	-99

TABLE 3. Changes in biogeoclimatic ecological zone distribution according to ensemble model CCGA1gax for the normal periods 2011–2040 (2025), 2041–2070 (2055), and 2071–2100 (2085).

Note: Elevation and north shifts are measured as averages of ecological zones within British Columbia, relative to averages modeled under 1961–1990 climate.

breakdown of statistics by ecological zones and maps is provided in Appendix C). The model fit statistic provided in this table is not comparable to the error of omission accuracy statistic of other studies, except in a purely descriptive sense. In our case, the statistic is just a different way of summarizing ecosystem misclassification rates (Table 3) and is not based on independent data. Our model fit for species ranges is quite comparable to other climate envelope type studies (Iverson and Prasad 1998), and one should note that at least a portion of that misclassification occurs at a very fine scale. Rates appear to be acceptable except for Pinus flexilis and Larix lyallii, which reach British Columbia only at the very northern tip of their ranges and occur only in a single variant. In those two cases the "lost habitat" and "frequency change" statistics are not meaningful. The other instance of a species occurring in a single variant is Quercus garryana. Neither are statistics meaningful for that species. In particular, the statistic "frequency change" cannot be reliable for species that are not well represented in British Columbia over several of BEC variants. However, we kept these species in the table to illustrate the method's limitations.

The maps and statistics reveal the following general trends: (1) many hardwoods that have their current northern range limit within British Columbia gain large amounts of new potential habitat, increase in frequency where they already occur, and rarely lose a significant amount of habitat, for example *Acer macrophyllum* (mapped in Appendix C: Fig. C4) for the coast and *Corylus cornuta* (Appendix C: Fig. C9) for the interior; (2) most hardwoods that already occur throughout British Columbia appear to be relatively unaffected in their overall frequency by climate change but could potentially occupy higher elevations, for example *Alnus tenuifolia* (Appendix C: Fig. C13); (3) some of the most important conifer species in British Columbia are

expected to significantly decrease in frequency and/or lose a large portion of their suitable habitat, for example Abies lasiocarpa (Appendix C: Fig. C3), Picea glauca (Appendix C: Fig. C11), Picea engelmanii, Picea mariana, and Pinus contorta (Appendix C: Fig. C12); (4) along with hardwoods, conifers that currently have a more southern distribution are expected to gain suitable habitat toward the north at a pace of at least 100 km per decade and to increase in frequency where they already occur, for example Abies grandis (Appendix C: Fig. C2), Pseudotsuga menziesii (Appendix C: Fig. C14) and Thuja plicata (Appendix C: Fig. C15); and (5) species that occur along elevation bands in mountainous terrain lose potential habitat faster than they gain new habitat and are expected to rapidly decline in frequency at their current elevations, for example Chamaecyparis nootkatensis (Appendix C: Fig. C8), Pinus albicaulis, and Tsuga mertensiana.

Predicted increases or decreases in species frequencies for each ecosystem will, of course, not literally be observed, even if climate changes over the next decades follow predictions. It is inherent to the analysis that we model the realized niche of species (and usually only a portion), while the fundamental (and potential) niche space is unknown. If the fundamental niche space of a particular species is much larger than the realized niche, there may not be any observable biological response. Mature individuals of all tree species have, in fact, a wide physiological tolerance to warmer climatic conditions. Nevertheless, a predicted decrease in frequency may be observable as (1) decreased growth rate of a species relative to others, (2) decreased natural recruitment, (3) higher reforestation failure for a species relative to others, or (4) increased disease problems or other types of mortality. Tree species highlighted in Appendix C: Table C1 can be used to contrast species with an opposite expected response within each ecosystem. For example, in the Sub-boreal Pine and Spruce

TABLE 4. Changes in tree species distribution and frequency according to ensemble model CCGA1gax for the normal periods 2011–2040 (2025), 2041–2070 (2055), and 2071–2100 (2085).

	Model Habitat lost (%)‡ N		New	habitat	(%)‡	Frequency change (%)§				
Species	Fit†	2025	2055	2085	2025	2055	2085	2025	2055	2085
Abies amabilis (Dougl. ex Loud.) Forbes	80	9	14	16	38	53	50	-10	-23	-47
Abies grandis (Dougl. ex D. Don) Lindl.	82	3	9	19	80	240	595	31	36	26
Abies lasiocarpa (Hook.) Nutt.	87	12	32	54	16	20	19	-24	-50	-75
Acer circinatum Pursh	50	26	38	35	77	166	272	12	41	74
Acer glabrum Torr.	76	8	10	24	57	100	127	43	102	79
Acer macrophyllum Pursh	77	1	2	3	77	149	216	31	69	97
Alnus tenuifolia Nutt.	81	13	17	31	25	36	52	-3	-24	-56
Alnus rubra Bong.	85	3	5	4	37	55	72	10	33	72
Alnus viridis (Chaix.) D. C.	84	12	24	47	22	29	32	-12	-32	-71
Arbutus menziesii Pursh	81	0	0	0	73	209	318	42	73	95
Betula neoalaskana Sarg.	82	12	34	71	16	6	1	1	-15	-59
Betula occidentalis Hook.	65	33	39	41	47	102	149	4	27	-19
Betula papyrifera Marsh.	83	7	9	5	41	53	66	64	80	62
Chamaecyparis nootkatensis (D. Don) Spach	82	11	16	21	24	33	31	-32	-55	-75
Cornus nuttallii Aud. ex T. & G.	70	2	3	4	80	154	229	20	53	88
Corvlus cornuta Marsh.	65	8	16	29	166	343	524	79	-25	-14
Crataegus spp.	49	55	53	51	122	198	468	-71	-54	-37
Juniperus scopulorum Sarg.	69	23	42	67	93	261	389	-5	-25	-64
Larix laricina (Du Roi) K. Koch	85	9	32	68	13	52	75	-4	-28	-65
Larix lvallii Parl.	28	84	98	100	58	38	19	-98	-100	-100
Larix occidentalis Nutt.	54	43	44	61	107	343	508	-17	-20	-49
Malus fusca (Raf.) Schneid.	85	3	5	3	48	74	86	64	77	43
Picea engelmannii Parry ex Engelm.	75	28	32	41	49	80	81	-7	-10	-55
Picea glauca (Moench) Voss	78	21	40	68	20	17	14	-23	-52	-77
Picea mariana (P. Mill.) B.S.P.	84	22	43	67	21	21	17	-7	-14	-42
Picea sitchensis (Bong.) Carr.	81		10	9	27	36	40	17	3	-29
Pinus albicaulis Engelm.	54	59	70	73	52	73	76	-66	-90	-98
Pinus contorta Dougl.	88	7	9	27	16	24	31	-13	-24	-50
Pinus flexilis Engelm.	19	89	100	100	108	381	218	-83	-100	-100
Pinus monticola Dougl ex D Don	66	10	10	10	80	178	227	24	52	39
Pinus nonderosa Dougl. ex P.& C. Lawson	68	15	6	ĩ	79	311	597	83	179	321
Populus halsamifera L	81	10	17	16	30	39	48	1	-8	-1
Populus tremuloides Michx.	85	9	12	22	18	25	34	15	-16	-43
Prunus emarginata (Dougl.) Walp.	57	21	28	32	130	279	488	24	55	80
Prunus pennsylvanica L. f.	59	41	76	97	54	42	17	-44	-78	-98
Prunus virginiana L.	70	11	3	1	69	126	212	14	55	142
Pseudotsuga menziesii (Mirbel) Franco	79	10	11	10	48	82	124	36	76	77
Ouercus garrvana Dougl.	81	Ő	0	0	73	209	318	0	Õ	0
Rhamnus purshiana DC.	57	19	29	29	113	219	282	17	48	74
Salix bebbiana Sarg.	79	19	18	28	26	37	49	-13	-25	-51
Salix discolor Muhl	67	38	79	95	85	56	20	-32	-64	-91
Salix lucida Muhl	52	41	55	71	69	81	77	-63	-66	-77
Salix scouleriana Barratt ex Hook	78	21	34	60	25	35	36	-29	-49	-76
Salix sitchensis Sanson ex Bong	56	33	46	38	56	76	71	-20	-51	-53
Taxus brevifolia Nutt.	81	8	.5	11	57	136	195	-8	-16	-39
Thuia plicata Donn ex D Don	82	5	5	8	54	94	124	14	24	32
Tsuga heterophylla (Raf.) Sarg.	77	6	5	7	47	90	109	6	1	-13
Tsuga mertensiana (Bong.) Carr.	66	29	48	73	34	37	37	-50°	-80	-91
	~ ~									

[†] Overlap of observed and predicted range as percentage of observed range.

‡ Overlap of observed and predicted range as percentage of current predicted range.

§ Change in frequency as percentage of current frequency, new habitat excluded from calculation.

|| Statistics for these species, particularly change in frequency, have limited meaning because they are based on a single ecosystem variant.

Zone (SBPS) of the interior plateau, we predict the largest decrease in frequency for *Pinus contorta*, while at the same time *Pseudotsuga menziesii* is predicted to increase in frequency. Systematic surveys of biological response that reflect these contrasting predictions could forcefully support (or reject) the hypothesis that observed biological changes are causally related to climate change.

Another interesting observation from this analysis is that species do not change their distribution or frequency in concert, which has similarly been concluded from fossil records (Webb 1987, Davis and Shaw 2001) and can be explained by niche theory (Jackson and Overpeck 2000). Differential reproductive rates and dispersal abilities may be important factors in determining the response of individual species to climate change, but modeling of the realized niche alone can account for independent geographical shifts of species, as well as for disassembly and reassembly of species into various communities under directional climate change. The study is a particularly good illustration of that effect because species response is not modeled separately, but is simply inferred from modeling the realized climate space of current ecosystems. Response to climate change is therefore not expected to be uniform throughout communities, and Parmesan and Yohe's (2003) finding that about one-third of the species reviewed had no statistically significant change in distribution does not appear to have been an unexpected result, even considering niche theory alone as an explanation.

CONCLUSIONS

We developed an ecosystem-based climate envelope modeling approach to assess potential climate change impact on forest ecosystems and tree species. The model was capable of predicting species ranges at high resolution far beyond the study area, including southern range limits and outlying populations for many species, which supports the view that climate is the primary factor controlling the distribution of plants. Four orthogonal canonical discriminant functions were required to describe the realized climate space for British Columbia's ecosystems and to model the realized niche space for tree species under current and predicted future climates.

Tree species within their northern range limits in British Columbia gained potential habitat at a pace of at least 100 km per decade; frequently occurring hardwoods appeared to be generally unaffected by climate change; and some of the most important conifer species in British Columbia were expected to lose a large portion of their suitable habitat. Despite the fact that response to climate change was not modeled separately for each species, species changed their distribution or frequency individualistically as expected from niche theory. The results supported the theoretical expectation that in community-wide surveys of biological response to climate change, a certain proportion of species will show no response or a reversed response.

The predicted spatial redistribution of realized climate space for British Columbia's ecosystems appears to be considerable even at the zone level, which represents major forest types. Ecosystems in mountainous areas appear to be particularly vulnerable, spatially shifting out of their current climatic envelope within 50 years. Other notable predictions are the initial expansion of the climatic envelope for Interior Cedar Hemlock within ~25 years, followed by expansion of the Interior Douglas-fir and Ponderosa Pine climate regions throughout the interior plateau replacing the current climate space of sub-boreal and boreal ecosystems.

The magnitude of predicted changes, climate change trends already observed in British Columbia, and presumed biological impacts, such as the current mountain pine beetle epidemic, strongly suggest that ecosystems and forest resources are threatened by continued global warming. If currently observed climate trends continue or accelerate, major changes to management of natural resources will become necessary. Because of modeling uncertainties at small spatial scales, systematic field monitoring of biological response to climate change guided by our model predictions may be the best indicator for the need to implement management changes.

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APPENDIX A

A table and seven figures illustrating model fit and model limitations (Ecological Archives E087-169-A1).

APPENDIX B

Three tables and three figures showing the effect of climate change on ecosystems (Ecological Archives E087-169-A2).

APPENDIX C

A table and 14 figures showing the effect of climate change on tree species (Ecological Archives E087-169-A3).

ELECTRONIC APPENDIX A. MODEL FIT AND MODEL LIMITATIONS

CONTENTS:

TABLE A1. Misclassification error rates
FIGURE A1. Maps of model fit
FIGURE A2. BEC zone extrapolation
FIGURE A3. Frequent – Interior: *Pinus contorta*FIGURE A4. Frequent – Coast: *Alnus rubra*FIGURE A5. Intermediate: *Pseudotsuga menziesii*FIGURE A6. Limited – Interior: *Pinus monticola*FIGURE A7. Limited – Coast: *Arbutus menziesii*

TABLE A1. Misclassification errors of discriminant analysis for each ecosystem. Underline

							То	Zone							
From zone:	Code	AT	BG	BWBS	CDF	CWH	ESSF	ICH	IDF	MH	MS	PP	SBPS	SBS	SWB
Alpine Tundra	AT	0.65	0.00	0.02	0.00	0.01	0.13	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.11
Bunch Grass	BG	0.00	<u>0.69</u>	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.13	0.00	0.00	0.00
Bor. Wh. and Bl. Spruce	BWBS	0.00	0.00	<u>0.91</u>	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.02
Coastal Douglas-Fir	CDF	0.00	0.00	0.00	<u>0.77</u>	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coastal W. Hemlock	CWH	0.00	0.00	0.00	0.01	<u>0.87</u>	0.02	0.01	0.00	0.08	0.01	0.00	0.00	0.00	0.00
Eng. Spruce - Subalp. Fir	ESSF	0.05	0.00	0.03	0.00	0.02	<u>0.72</u>	0.05	0.00	0.02	0.04	0.00	0.00	0.04	0.03
Interior Cedar Hemlock	ICH	0.00	0.00	0.01	0.00	0.02	0.11	0.60	0.06	0.00	0.03	0.01	0.00	0.15	0.00
Interior Douglas-Fir	IDF	0.00	0.04	0.00	0.00	0.02	0.00	0.03	<u>0.69</u>	0.00	0.06	0.07	0.04	0.05	0.00
Mountain Hemlock	MH	0.15	0.00	0.00	0.00	0.28	0.15	0.01	0.00	<u>0.40</u>	0.00	0.00	0.00	0.00	0.01
Mountain Spruce	MS	0.00	0.00	0.00	0.00	0.01	0.13	0.10	0.11	0.00	<u>0.49</u>	0.00	0.06	0.09	0.00
Ponderosa Pine	PP	0.00	0.36	0.00	0.00	0.00	0.00	0.02	0.19	0.00	0.00	<u>0.44</u>	0.00	0.00	0.00
Sub-Bor. Pine and Spruce	SBPS	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.17	0.00	0.04	0.00	0.65	0.11	0.00
Sub-Bor. Spruce	SBS	0.00	0.00	0.02	0.00	0.00	0.06	0.13	0.02	0.00	0.02	0.00	0.06	<u>0.68</u>	0.00
Spruce - Willow - Birch	SWB	0.12	0.00	0.16	0.00	0.00	0.15	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.56

indicates correct classification, bold highlights the error rates larger than 5%.

FIGURE A1. Mapped BEC zones (left) and predicted BEC zones using 1.25 arcmin PRISM data for the 1961-1900 normal period (top right) and 400m resolution climate data (bottom right). BEC variants are predicted with discriminant analysis. For clarity, only zones are delineated below. In the prediction maps the original zone boundaries are left in the image to better evaluate the match of predictions.





FIGURE A2. Extrapolation of BEC zones based on elevation-adjusted PRISM climate data for the 1961-1990 normal period. Dotted areas indicate that there is no match to climatic conditions observed in British Columbia. The color of dots indicates which zone has the closest match. The topography of the region is given as a reference.



FIGURE A3. Testing of model limitation by extrapolation of species ranges south based on elevation-adjusted PRISM climate data for the 1961-1990 normal period. Example for interior – frequent species: *Pinus contorta* (frequency for predicted map: $\leq 5\%$, $\leq 5-10\%$, $\leq >10\%$).



FIGURE A4. Testing of model limitation by extrapolation of species ranges south based on elevation-adjusted PRISM climate data for the 1961-1990 normal period. Example for coast – frequent species *Alnus rubra* (frequency for predicted map: $\leq 2\%$, $\leq 2\%$).



FIGURE A5. Testing of model limitation by extrapolation of species ranges south based on elevation-adjusted PRISM climate data for the 1961-1990 normal period. Example half of the range in British Columbia: *Pseudotsuga menziesii* (frequency for predicted map: ■ <5%, ■ 5-10%, ■ >10%).



FIGURE A6. Testing of model limitation by extrapolation of species ranges south based on elevation-adjusted PRISM climate data for the 1961-1990 normal period. Example for interior – small portion in BC: *Larix occidentalis* (frequency for predicted map: $\leq 2\%$, $\leq 2\%$).



FIGURE A7. Testing of model limitation by extrapolation of species ranges south based on elevation-adjusted PRISM climate data for the 1961-1990 normal period. Example for coast – small portion in BC: *Arbutus menziesii* (frequency for predicted map: $\leq 1\%$, $\leq 1\%$).



ELECTRONIC APPENDIX B. EFFECT OF CLIMATE CHANGE ON ECOSYSTEMS

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TABLE B1. "From – to" statistics for 2025.
TABLE B2. "From – to" statistics for 2055.
TABLE B3. "From – to" statistics for 2085.
FIGURE B1. Detail: Southern Coast Mountains
FIGURE B2. Detail: Northern Rocky Mountains.
FIGURE B3. Other GCMs, Sensitivity analysis

	AT	Alpine Tundra
Lower	montane	
	MH	Mountain Hemlock (coastal)
	ESSF	Engelmann Spruce - Subalpine Fir (interior)
	MS	Mountain Spruce (interior - below ESSF)
	SWB	Spruce - Willow - Birch (north)
Interior	(approx. so	uth to north)
	BG	Bunch Grass
	PP	Ponderosa Pine
	IDF	Interior Douglas-Fir
	ICH	Interior Cedar Hemlock (high precipitation)
	SBPS	Sub-Boreal Pine and Spruce
	SBS	Sub-Boreal Spruce
	BWBS	Boreal White and Black Spruce
<u>Coast (</u>	south to nor	<u>th)</u>
	CDF	Coastal Douglas-Fir
	CWH	Coastal Western Hemlock

Color Coding

							То	Zone							
From zone:	Code	AT	BG	BWBS	CDF	CWH	ESSF	ICH	IDF	MH	MS	PP	SBPS	SBS	SWB
Alpine Tundra	AT	<u>0.39</u>	0.00	0.01	0.00	0.02	0.39	0.00	0.00	0.09	0.01	0.00	0.00	0.00	0.09
Bunch Grass	BG	0.00	<u>0.95</u>	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.04	0.00	0.00	0.00
Bor. Wh. and Bl. Spruce	BWBS	0.00	0.00	0.84	0.00	0.00	0.03	0.02	0.01	0.00	0.00	0.00	0.00	0.09	0.01
Coastal Douglas-Fir	CDF	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coastal W. Hemlock	CWH	0.00	0.00	0.00	0.02	<u>0.96</u>	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00
Eng. Spruce - Subalp. Fir	ESSF	0.02	0.00	0.01	0.00	0.04	<u>0.59</u>	0.18	0.00	0.02	0.05	0.00	0.01	0.08	0.00
Interior Cedar Hemlock	ICH	0.00	0.01	0.02	0.00	0.01	0.00	0.82	0.10	0.00	0.01	0.00	0.00	0.02	0.00
Interior Douglas-Fir	IDF	0.00	0.10	0.00	0.00	0.01	0.00	0.04	<u>0.66</u>	0.00	0.01	0.14	0.00	0.04	0.00
Mountain Hemlock	MH	0.03	0.00	0.01	0.00	0.54	0.01	0.00	0.00	0.41	0.00	0.00	0.00	0.00	0.00
Mountain Spruce	MS	0.00	0.00	0.00	0.00	0.10	0.08	0.11	0.29	0.00	0.26	0.00	0.11	0.05	0.00
Ponderosa Pine	PP	0.00	0.64	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	<u>0.35</u>	0.00	0.00	0.00
Sub-Bor. Pine and Spruce	SBPS	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.29	0.00	0.05	0.00	<u>0.31</u>	0.29	0.00
Sub-Bor. Spruce	SBS	0.00	0.00	0.00	0.00	0.00	0.00	0.46	0.09	0.00	0.03	0.00	0.01	0.40	0.00
Spruce - Willow - Birch	SWB	0.01	0.00	0.31	0.00	0.01	0.51	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.13

TABLE B1. Shift of the climatic envelopes of ecological zones by 2025 according to ensemble model CCGA1gax. <u>Underline</u> indicates the unchanged proportion when compared to the 1961-1990 baseline simulation, **bold** highlights changes larger than 10%.

TABLE B2. Shift of the climatic envelopes of ecological zones by 2055 according to ensemble model CCGA1gax. <u>Underline</u> indicates the unchanged proportion when compared to the 1961-1990 baseline simulation, **bold** highlights changes larger than 10%.

							То	Zone							
From zone:	Code	AT	BG	BWBS	CDF	CWH	ESSF	ICH	IDF	MH	MS	PP	SBPS	SBS	SWB
Alpine Tundra	AT	0.27	0.00	0.01	0.00	0.04	0.56	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.03
Bunch Grass	BG	0.00	<u>0.96</u>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
Bor. Wh. and Bl. Spruce	BWBS	0.00	0.03	<u>0.65</u>	0.00	0.00	0.03	0.02	0.14	0.00	0.01	0.01	0.00	0.11	0.00
Coastal Douglas-Fir	CDF	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coastal W. Hemlock	CWH	0.00	0.00	0.00	0.05	<u>0.93</u>	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Eng. Spruce - Subalp. Fir	ESSF	0.02	0.00	0.03	0.00	0.11	0.37	0.36	0.02	0.01	0.08	0.00	0.01	0.01	0.00
Interior Cedar Hemlock	ICH	0.00	0.04	0.00	0.00	0.02	0.00	0.70	0.21	0.00	0.00	0.03	0.00	0.00	0.00
Interior Douglas-Fir	IDF	0.00	0.25	0.00	0.00	0.02	0.00	0.08	0.42	0.00	0.00	0.23	0.00	0.00	0.00
Mountain Hemlock	MH	0.03	0.00	0.00	0.00	0.84	0.01	0.01	0.00	<u>0.10</u>	0.00	0.00	0.00	0.00	0.00
Mountain Spruce	MS	0.00	0.00	0.00	0.00	0.10	0.03	0.09	0.45	0.00	0.14	0.00	0.08	0.12	0.00
Ponderosa Pine	PP	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sub-Bor. Pine and Spruce	SBPS	0.00	0.01	0.00	0.00	0.00	0.00	0.05	0.77	0.00	0.01	0.00	0.00	0.16	0.00
Sub-Bor. Spruce	SBS	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.47	0.00	0.01	0.04	0.00	0.05	0.00
Spruce - Willow - Birch	SWB	0.01	0.00	0.23	0.00	0.02	0.59	0.03	0.00	0.00	0.00	0.00	0.00	0.11	0.00

							То	Zone							
From zone:	Code	AT	BG	BWBS	CDF	CWH	ESSF	ICH	IDF	MH	MS	PP	SBPS	SBS	SWB
Alpine Tundra	AT	0.21	0.00	0.00	0.00	0.10	0.60	0.01	0.00	0.05	0.02	0.00	0.00	0.00	0.00
Bunch Grass	BG	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bor. Wh. and Bl. Spruce	BWBS	0.00	0.00	<u>0.14</u>	0.00	0.00	0.02	0.05	0.26	0.00	0.01	0.44	0.00	0.08	0.00
Coastal Douglas-Fir	CDF	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coastal W. Hemlock	CWH	0.00	0.00	0.00	0.10	<u>0.89</u>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eng. Spruce - Subalp. Fir	ESSF	0.01	0.00	0.01	0.00	0.16	<u>0.10</u>	0.54	0.09	0.00	0.07	0.00	0.00	0.01	0.00
Interior Cedar Hemlock	ICH	0.00	0.10	0.00	0.00	0.02	0.00	0.68	0.04	0.00	0.00	0.16	0.00	0.00	0.00
Interior Douglas-Fir	IDF	0.00	0.50	0.00	0.00	0.01	0.00	0.09	0.10	0.00	0.00	0.30	0.00	0.00	0.00
Mountain Hemlock	MH	0.03	0.00	0.00	0.00	0.94	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Mountain Spruce	MS	0.00	0.00	0.00	0.00	0.14	0.00	0.33	0.33	0.00	0.04	0.07	0.00	0.08	0.00
Ponderosa Pine	PP	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sub-Bor. Pine and Spruce	SBPS	0.00	0.08	0.00	0.00	0.00	0.00	0.04	0.74	0.00	0.00	0.11	0.00	0.03	0.00
Sub-Bor. Spruce	SBS	0.00	0.02	0.00	0.00	0.00	0.00	0.24	0.44	0.00	0.00	0.29	0.00	0.01	0.00
Spruce - Willow - Birch	SWB	0.01	0.00	0.23	0.00	0.03	0.39	0.17	0.00	0.00	0.09	0.00	0.00	0.08	0.00

TABLE B3. Shift of the climatic envelopes of ecological zones by 2085 according to ensemble model CCGA1gax. <u>Underline</u> indicates the unchanged proportion when compared to the 1961-1990 baseline simulation, **bold** highlights changes larger than 10%.

FIGURE B1. Detailed view of the shift of the climatic envelopes of ecological zones based on an ensemble simulation CGCM1gax of the Canadian Centre for Climate Modelling and Analysis.







FIGURE B2. Detailed view of the shift of the climatic envelope of ecological zones based on an ensemble simulation CGCM1gax of the Canadian Centre for Climate Modelling and Analysis.









FIGURE B3. Shift of climatic envelope of ecological zones according to different global circulation models and as a result of simple modifications to all temperature and/or precipitation variables in order to test the sensitivity of the model.



+2°C

-10% / +2°C

+10% / +2°C



+25% / +2°C

+50% / +2°C

+100% / $+2^{\circ}C$



ELECTRONIC APPENDIX C. EFFECT OF CLIMATE CHANGE ON TREE SPECIES

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TABLE C1.	Change statistics by BEC zone
FIGURE C1.	Maps and statistics for Abies amabilis
FIGURE C2.	Maps and statistics for Abies grandis
FIGURE C3.	Maps and statistics for Abies lasiocarpa
FIGURE C4.	Maps and statistics for Acer macrophyllum
FIGURE C5.	Maps and statistics for Alnus tenuifolia
FIGURE C6.	Maps and statistics for Alnus rubra
FIGURE C7.	Maps and statistics for <i>Betula papyrifera</i>
FIGURE C8.	Maps and statistics for Chamaecyparis nootkatensis
FIGURE C9.	Maps and statistics for Corylus cornuta
FIGURE C10.	Maps and statistics for Larix occidentalis
FIGURE C11.	Maps and statistics for <i>Picea glauca</i>
FIGURE C12.	Maps and statistics for <i>Pinus contorta</i>
FIGURE C13.	Maps and statistics for <i>Populus balsamifera</i>
FIGURE C14.	Maps and statistics for <i>Pseudotsuga menziesii</i>
FIGURE C15.	Maps and statistics for <i>Thuja plicata</i>

Explanation of statistics given with each set of maps

Correctly predicted habitat based on current climate (1961-1990 normals) as a percentage of the observed species range. Note that some of these errors occur at very small scales (400m resolution) and are therefore not visible in these images.

This is the area predicted as unsuitable habitat for the species under climate change as a proportion of the total current habitat (modeled as a function of 1961-1990 climate normals).

The area predicted as suitable habitat under climate change, where the species is currently not present (note that the species is unlikely to colonize most of this area within a few decades, except perhaps across short distances along elevational gradients).

A weighted average of predicted frequency changes where the species is already present (New habitat is excluded from this calculation, because it is unlikely that the species will colonize most of this area)

These are the largest predicted frequency changes in units of percentage points by ecosystem. This example suggests that response of this species to climate change will most likely be observable in the CWH and ESSF ecosystems.



TABLE C1. Changes in tree species frequency in percentage points by 2055 relative to the 1961-1990 normal period, broken down by ecological zone. (New habitat excluded from calculation except for Alpine Tundra (AT); **bold** indicates an increase by more than 100% <u>underline</u> a larger than 90% decrease (not applicable to Alpine Tundra, which is assumed to have a frequency of zero for the 1961-1990 period).

	BEC Zone												
Species	AT	BG	BWBS	CWH	ESSF	ICH	IDF	MH	MS	PP	SBPS	SBS	SWB
Abies amabilis	2.1			-5.6	9.9	-1.9	0.0	-0.3					
Abies grandis				0.5		0.0	-0.7						
Abies lasiocarpa	8.7		-0.2	-1.6	-9.9	-4.2	<u>-0.1</u>	-3.0	-3.6		0.4	-4.4	-0.3
Acer circinatum				1.1			-1.1						
Acer glabrum		-0.2		0.0	0.1	0.8	0.0		1.4	-1.2		1.3	
Acer macrophyllum				1.1			0.4						
Alnus rubra				0.9			0.5						
Alnus tenuifolia	0.1	-0.2	-0.1	-0.8	0.1	-0.9	-0.2		0.1	-0.2	0.3	-0.8	
Alnus viridis	0.7		-0.9	-1.4	0.2	-0.6	-0.2	-0.7	-0.4		-0.1	-1.0	1.1
Arbutus menziesii				1.1									
Betula neoalaskana			0.0										
Betula occidentalis		0.0		-0.5	-0.1	0.0	0.3		-0.1	-0.3		0.2	0.0
Betula papyrifera		0.1	0.0	0.1	0.3	1.1	0.0		2.4	-0.5	2.6	1.7	
Chamaecyparis nootkatensis	0.6			-3.0	-0.2			-4.3					
Cornus nuttallii				0.2			0.0						
Corylus cornuta				-0.1	0.3	0.2	-0.1			-0.2		-1.9	
Crataegus species		0.1		0.0		0.0	-0.2			0.1			
Juniperus scopulorum		-0.4			0.1	0.0	-0.1		0.0	-0.2		0.0	
Larix laricina	0.1		-0.2		-0.7								
Larix lyallii					-2.2								
Larix occidentalis					0.8	-0.6	-1.9		0.9	<u>-1.5</u>			
Malus fusca				0.2									
Picea engelmannii	3.4		-1.5	-0.7	0.0	-1.1	-1.1		-2.1	-0.6	-0.2	0.5	
Picea glauca	0.6		-3.0		-0.2	-0.3	-0.6		-0.1		0.4	-2.2	-5.2
Picea mariana	0.6		-1.1		1.6	-0.4					-2.1	-2.1	2.2
Picea sitchensis	0.1			-0.3		-0.5		1.6					
Pinus albicaulis	0.7				-1.6	-0.1	-0.1		-0.1	0.0			
Pinus contorta	2.0		-0.7	-0.1	0.7	0.0	-2.9	0.6	-8.4	<u>-0.7</u>	-7.9	-3.7	2.4
Pinus flexilis					0.0		-0.1						
Pinus monticola				0.0	0.5	0.2	0.0	0.0	0.9				
Pinus ponderosa		0.1			0.2	3.4	4.9		1.5	1.2			
Populus balsamifera	0.1	0.9	-0.5	0.3	0.3	-0.2	0.5		0.3	0.8	0.4	0.0	-0.9
Populus tremuloides	0.2	-0.4	-1.8	-0.2	0.5	-0.2	-1.2		1.3	-0.4	1.3	-0.3	0.5
Prunus emarginata		<u>0.0</u>		0.0		0.0	0.0			<u>0.0</u>			
Prunus pensylvanica			0.0			0.0	<u>-0.1</u>			<u>-0.1</u>		0.0	
Prunus virginiana		0.2	-0.1			0.1	0.2		0.0	0.3		0.0	
Pseudotsuga menziesii	0.2	-1.4		6.1	3.3	6.6	-4.8		10.0	<u>-6.9</u>	11.1	10.7	
Quercus garryana													
Rhamnus purshiana				0.0		0.0	0.0						
Salix bebbiana		0.0	0.0	-0.1	0.0	-0.1	-0.1		0.0	0.2	0.0	-0.1	0.0
Salix discolor		-0.2	0.0		0.0	0.0	0.0		<u>-0.1</u>		0.0	0.0	
Salix lucida		-0.1	0.0	-0.1	0.0	<u>-0.3</u>	-0.2					-0.8	
Salix scouleriana	0.1	-0.1	-0.2	-0.1	-0.1	-0.2	-0.3		0.1		0.1	-0.1	-0.5
Salix sitchensis				0.0	0.3	<u>-1.5</u>		-0.3	-0.2			<u>-1.3</u>	
Taxus brevifolia				0.0		-0.3	0.1		0.1				
Thuja plicata	0.2			1.1	9.5	-4.8	-1.1	10.1	10.2	<u>-0.4</u>		10.1	
Tsuga heterophylla	1.0			-6.5	18.3	-9.9	2.4	23.0				11.2	
Tsuga mertensiana	2.2			-1.6	-5.0	-0.6		<u>-19</u>					



FIGURE C1. Observed and predicted range and frequency for *Abies amabilis* (Dougl. ex Loud.) Dougl. - Amabilis fir ($\leq <5\%$, $\leq 5-10\%$, $\leq >10\%$)



FIGURE C2. Observed and predicted range and frequency for *Abies grandis* (Dougl. ex D. Don) Lindl. - Grand fir ($\leq 5\%$, $\leq 5-10\%$, $\leq >10\%$).



FIGURE C3. Observed and predicted range and frequency for *Abies lasiocarpa* (Hook.) Nutt. - Subalpine fir ($\leq <10\%$, $\leq 10-20\%$, $\leq >20\%$)



FIGURE C4. Observed and predicted range and frequency for *Acer macrophyllum* Pursh - Bigleaf maple ($\leq 5\%$, $\leq 25\%$).



FIGURE C5. Observed and predicted range and frequency for *Alnus tenuifolia* Nutt. - Mountain alder ($\leq 1\%$, $\leq 1\%$).



FIGURE C6. Observed and predicted range and frequency for *Alnus rubra* Bong. - Red alder (■ <2%, ■ ≥2%).



FIGURE C7. Observed and predicted range and frequency for *Betula papyrifera* Marsh. - Paper birch (■ <1%, ■ 1-2%, ■ >2%).



FIGURE C8. Observed and predicted frequency for *Chamaecyparis nootkatensis* (D. Don) Spach - Yellow-cedar (< <5%, < 5-10%, < >10%).



FIGURE C9. Observed and predicted range and frequency for *Corylus cornuta* Marsh. - Hazelnut ($\leq 1\%$, $\leq 1\%$).



FIGURE C10. Observed and predicted range and frequency for *Larix occidentalis* Nutt. - Western larch ($\leq 2\%$, $\leq 2\%$).



FIGURE C11. Observed and predicted range and frequency for *Picea glauca* (Moench) Voss - White spruce (< <5%, < 5-10%, < >10%).



FIGURE C12. Observed and predicted range and frequency for *Pinus contorta* Dougl. - Lodgepole pine (< <5%, < 5-10%, < >10%).



FIGURE C13. Observed and predicted range and frequency for *Populus balsamifera* L. - Balsam poplar (■ <1%, ■ 1-2%, ■ >2%).



FIGURE C14. Observed and predicted range and frequency for *Pseudotsuga menziesii* (Mirbel) Franco - Douglas-fir (< <5%, < 5-10%, < >10%).



FIGURE C15. Observed and predicted range and frequency for *Thuja plicata* Donn ex D. Don - Western redcedar ($\leq 5\%$, $\leq 5-10\%$, $\leq >10\%$).