Tracking suitable habitat for tree populations under climate change in western North America

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Abstract An important criticism of bioclimate envelope models is that many wide-ranging species consist of locally adapted populations that may all lag behind their optimal climate habitat under climate change, and thus should be modeled separately. Here, we apply a bioclimate envelope model that tracks habitat of individual populations to estimate adaptational lags for 15 wide-ranging forest tree species in western North America. An ensemble classifier modeling approach (RandomForest) was used to spatially project the climate space of tree populations under observed climate trends (1970s to 2000s) and multi-model projections for the 2020s, 2050s and 2080s. We find that, on average, populations already lag behind their optimal climate niche by approximately 130 km in latitude, or 60 m in elevation. For the 2020s we expect an average lag of approximately 310 km in latitude or 140 m in elevation, with the most pronounced geographic lags in the Rocky Mountains and the boreal forest. We show that our results could in principle be applied to guide assisted migration of planting stock in reforestation programs using a general formula where 100 km north shift is equivalent to approximately 44 m upward shift in elevation. However, additional non-climatic factors should be considered when matching reforestation stock to suitable planting environments.

1 Introduction

Bioclimate envelope models, also referred to as species distribution models, have emerged as a widely used modeling technique to illustrate the discrepancy between current species distributions and their predicted potential habitat under climate change (e.g. Overpeck et al. 1991; Thomas et al. 2004). Bioclimate envelope models correlate species census data with environmental predictor variables using a wide range of statistical and machine-learning methods (e.g. reviewed by Guisan and Zimmermann 2000). The limitations and weaknesses

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of the bioclimate envelope model approach have been thoroughly discussed and the general consensus is that bioclimate envelope projections should not be literally interpreted as predicted demographic response of species to climate change, and that loss of habitat predicted by bioclimate envelope models does not necessarily entail extirpation of current populations (e.g. Botkin et al. 2007; Hampe 2004; Thuiller et al. 2008).

Despite their limitations for modeling demographic response, bioclimate envelope models can still be useful for a conceptually much simpler practical task: guiding climate change adaptation strategies for forestry that involve habitat restoration, reforestation, or conservation objectives (Gray et al. 2011). For such management applications, the primary task is to match the correct planting stock with anticipated climate conditions, rather than to predict complex demographic processes and biological interactions under changing climate. However, selecting appropriate planting stock not only requires choosing an appropriate species but also genotypes of locally adapted populations that match anticipated planting environments (e.g. Ying and Yanchuk 2006). Therefore, we need to include genetic structure of species in bioclimate envelope models.

In widespread tree species, genetically differentiated populations are uniquely and often narrowly adapted to their local environments (Morgenstern 1996). Hence, climate change impacts will not be limited to the trailing edge of a species range, but instead may apply to populations throughout the species range. Under climate change, all populations may occupy environments at or beyond the margins of their individual climate niches (Davis and Shaw 2001; Hampe 2004; Millar et al. 2007). This is also supported by empirical evidence suggesting that genetic population structure in widespread forest trees should not be ignored. For example, O'Neill et al. (2008) and Wang et al. (2006b, 2010) found that when genetic structure was considered, the predicted growth and survival of locally adapted lodgepole pine (*Pinus contorta*) populations was reduced. Chen et al. (2010) found that northern and high elevation Douglas-fir (*Pseudotsuga meniesii*) populations are more vulnerable to climate change than the populations from the southern end of the species range, presumably due to narrow genetic adaptation of local populations.

In this study we illustrate how genetic population structure can be integrated in bioclimate envelope modeling by using ecosystem delineations as modeling units, which serve as proxy for locally adapted species populations. For practical applications of seed movement, we can then identify the geographic origin of locally adapted populations that best match the anticipated future climate. In this study we project suitable habitat for populations of 15 wide-ranging tree species in western North America under observed and projected climate change. Our objective is to determine how far populations already lag behind their assumed optimal climate habitat, and how these adaptational lags of populations are predicted to change in the future.

2 Materials and methods

To generate future habitat projections for individual populations we build on an ecosystem-based modeling technique developed by Hamann and Wang (2006). This approach uses climate variables to characterize multivariate climate conditions within delineated ecosystem polygons. Ecosystem units are the dependent class variable in this modeling approach. Although soil and topographic variables could be added as predictors (e.g. Mbogga et al. 2010), we choose to exclude static variables from this modeling effort. Therefore, ecosystem delineations simply serve as modeling units that represent relatively homogenous climate conditions. Species distributions are subsequently derived by replacing the predicted ecosystem unit with species' probability of presence or frequency values calculated from sample

plot data as explained in more detail below. In this study, we extend this approach by using the ecosystem modeling units as a proxy for tree populations. This assumes that genetic differentiation within species is largely accounted for by ecosystem delineations. Transferring planting material within such ecosystem delineations would usually not be associated with significant reduction in growth and survival relative to local sources (Ying and Yanchuk 2006; Hamann et al. 2005, 2011).

2.1 Bioclimate envelope modeling

Predictions of ecosystem classes were carried out with an ensemble classification tree analysis implemented by the RandomForest software package (Breiman 2001) for the R programming environment (R Development Core Team 2008). RandomForest grows multiple classification trees from bootstrap samples of the training data and determines the predicted class by majority vote over all classification trees (Cutler et al. 2007). Importance values for predictor variables were calculated as the number of times that a climate variable contributed to a correct classification in a bootstrapped cross-validation procedure with different permutations of predictor variables. As dependent variable, we use 770 fine-scale ecosystem delineations for western North America as described in Roberts and Hamann (2012). From each ecosystem we randomly sampled 100 1 km grid cells, which were climatically characterized, and subsequently used as training data for classification tree analysis.

2.2 Baseline climate data and future projections

For climatic characterization of ecosystems we use interpolated climate data that were generated with the Parameter Regression of Independent Slopes Model (Daly et al. 2008). These surfaces were derived from climate normal data observed at weather stations in the United States and Canada for the 1961–1990 period. This database was enhanced with lapse-rate based down-sampling to 1 km resolution and an estimation of biologically relevant climate variables (Mbogga et al. 2009). From this dataset of more than 50 monthly, seasonal, and annual climate variables, we chose ten predictor variables that are biologically important and that had relatively low collinearity. These included mean annual temperature, mean warmest month temperature, mean coldest month temperature, continentality (difference between mean January and mean July temperature), mean annual precipitation, growing season precipitation (May to September), the number of frost free days and the number of growing degree days above 5 °C. All of these variables are described in detail by Wang et al. (2006a). We also included two dryness indices that are based on estimates of potential evapotranspiration and water deficit: annual and summer climate-moisture indices according to Hogg (1997).

Climate projections for western North America for the 2020s, 2050s, 2080s were generated by overlaying projections from general circulation models expressed as the difference from the 1961–1990 normal period. For each future period, 18 climate projections base on four major Special Report on Emissions Scenarios (SRES) families (AIFI, A2, B1, B2), implemented by five modeling groups (CGCM, Canada; CSIRO2, Australia, HADCM3; United Kingdom; ECHAM4, Europe; and PCM, United States) were used. Model-emission scenario combinations ECHAM4-A1FI and ECHAM4-B1 were unavailable resulting in a total of 18 future projections per time period. To represent recent climate trends we use the 1997–2006 decadal average, which can be interpreted as observed climate change over a 25-year period (the mid-point of the 1961–1990 climate baseline period and

the mid-point of the recent decadal average: 1975 to 2000). For more details refer to Mbogga et al. (2009) and Wang et al. (2012).

2.3 Tree species inventory data

For species and population level analysis we selected 15 major forest tree species of commercial importance in western North America: pacific silver fir (*Abies amabilis* Douglas ex J. Forbes), Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Sudworth), tamarack (*Larix laricina* (Du Roi) K. Koch), western larch (*Larix occidentalis* Nuttall), Engelmann spruce (*Picea engelmannii var. engelmannii* Parry ex Engelmann), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Miller) Britton), Sitka spruce (*Picea sitchensis* (Bongard) Carrière), lodgepole pine (*Pinus contorta* Douglas ex Loudon), western white pine (*Pinus monticola* Douglas ex D. Don in Lambert), ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western red-cedar (*Thuja plicata* Donn ex D. Don in Lambert), western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent), and trembling aspen (*Populus tremuloides* Michaux). The scientific names are according to the Flora of North America Editorial Committee (1993+).

Species frequency across western North America was determined with approximately 30,000 forest inventory plots from western Canada (Hamann and Wang 2005) and approximately 18,000 forest inventory plots from the western United States (Bechtold and Patterson 2005). As a common measure of species frequency, we use an estimated percent areal cover of the canopy projected to the ground, scaled by the total canopy cover of the forest inventory plot. Since this measure was not available for data from the western United States, we used percent basal area as a proxy for frequency as in Schroeder et al. (2010). Species frequencies for each ecosystem were calculated as average across all sample plots that fall within an ecosystem polygon. We also calculated probability of presence of a species for each ecosystem unit. This was simply the proportion of inventory plots across all sample points where the species was present.

2.4 Model evaluation

We use a receiver operating characteristics (ROC) curve of the predicted probability of species presence to evaluate the statistical accuracy of the bioclimate envelope model for individual species. Overall model performance was evaluated by the area under the ROC curve (AUC), which represents the probability that the model classifier will correctly identify a randomly chosen true species presence (Fawcett 2006; Fielding and Bell 1997). The AUC of the ROC curve balances the ability of the model to detect a species when it is present (sensitivity) against its ability to not predict a species when it is absent (specificity). We further report model sensitivity and specificity, which were reported as an average over a full range of thresholds between zero and one. All ROC and AUC calculations were carried out with the ROCR package (Sing et al. 2005) for the R programming environment (R Development Core Team 2008).

3 Results

3.1 Variable importance and model accuracy

RandomForest importance values indicate that most climate predictors have fairly equal roles in habitat predictions, with growing season precipitation, mean annual precipitation,

and continentality being higher contributors to classifications (Table 1). Temperature related variables that describe the growing season apparently contribute less to the classification analysis. The most important variable to differentiate among western North American ecosystems in a classification tree analysis was found to be mean growing season precipitation, followed by mean annual precipitation, which is fairly highly correlated ($r=0.79$).

Model evaluation statistics for species presence/absence predictions are shown in Table 2. Except for the wide-ranging tree species, the total error rate of false positives and false negatives is low, in the single digit percentage range. AUC values are consistently high, ranging from 0.81 to 0.95, again with species that have restricted distributions having the best predictive accuracy (e.g. Sitka spruce). For the majority of species, the number of false negative errors is higher than the number of false positive errors, indicating that model prediction error is predominantly driven by omission error, or falsely predicting species absence. Similarly, model sensitivity, or the proportion of true species presences, is low and model specificity is high for all species, indicating that true species absences were well modeled.

3.2 Habitat projections and uncertainty

The first row of maps in Fig. 1 illustrates the shift in projected ecosystem modeling units that contain Douglas-fir under recent climate change. We indicate aggregated ecosystem modeling units with different colors representing major ecosystem classes. The second row of Fig. 1 illustrates the expected frequency of Douglas fir under the 1961–1990 baseline and under climate change trends observed over the last 25 years, represented by a recent decadal average (1997–2006 relative to the 1961–1990 baseline). Similar maps in first row of Fig. 2 indicates where Douglas-fir climate conditions would generally be suitable for the species to represent a major forest component in the future, based on an average of predictions for a variety of climate change scenarios. A low average frequency could therefore represent either a low frequency in most model runs or a higher frequency in few model runs. The second row of Fig. 2 quantifies uncertainty in habitat projections for the 2020s, 2050s, and 2080s. Red and blue indicate complete model agreement for absence and presence respectively. Intermediate shades indicate areas of uncertainty, which substantially increase towards the 2080s. In the example for Douglas-fir, by the end of the century uncertainty for the interior distribution appears to be so high that no reliable predictions can be made: over large

Table 1 Importance of predictor climate variables in RandomForest predictions of ecosystem modeling units for western North America. Importance values for predictor variables were calculated as the number of times that a climate variable contributed to a correct classification in a bootstrapped cross-validation procedure with different permutations of predictor variables

Climate variable	RF importance
Mean annual temperature (°C)	6424
Mean warmest month temperature (°C)	5835
Mean coldest month temperature (°C)	7974
Continentality (°C)	8463
Mean annual precipitation (mm)	9049
Growing season precipitation (mm)	9825
Climate moisture index (cm)	7134
Growing season climate moisture index (cm)	6352
Degree days >5 °C (days)	6862
Frost free period (days)	6811

Table 2 Sampling and biogeographical information for species, as well as statistics that describe the predictive accuracy of the species distribution model for 15 major forest tree species in western North America

Species	Present[a]	Range (sqkm)	Relative abundance[b]	Error rate[c]	Model specificity	Model sensitivity	AUC
Black spruce	4489	710,748	0.14	0.07	0.88	0.58	0.90
Douglas-fir	8808	1,002,592	0.21	0.12	0.86	0.60	0.88
Engelmann spruce	6223	581,058	0.09	0.10	0.86	0.56	0.81
Lodgepole pine	11275	1,016,718	0.13	0.19	0.77	0.61	0.82
Pacific silver fir	1615	172,348	0.16	0.02	0.95	0.64	0.93
Ponderosa pine	3967	591,394	0.23	0.06	0.93	0.59	0.88
Sitka spruce	1016	217,983	0.21	0.02	0.95	0.65	0.95
Tamarack	406	324,392	0.03	0.01	0.91	0.61	0.93
Trembling Aspen	7241	1,135,473	0.14	0.12	0.76	0.64	0.83
Western hemlock	4860	362,021	0.19	0.05	0.94	0.67	0.94
Western larch	821	119,669	0.05	0.01	0.95	0.54	0.86
Western redcedar	3798	305,163	0.08	0.06	0.92	0.68	0.94
Western white pine	820	185,919	0.02	0.01	0.92	0.60	0.89
White spruce	7115	848,866	0.10	0.11	0.84	0.61	0.88

[a] Out of approximately 54,716 sample plots, including non-forested plots

[b] Expected proportion of basal area or crown cover when present in a sample plot

[c] Error Rate=(False Positive + False Negative)/(Total Positive +Total Negative)

areas approximately half the models project species presence and half predict absence of suitable species habitat.

Species frequency projections and maps of model uncertainty for all other species are provided as Online Resources 1–15. Notable observations are the projection of substantial loss of climate habitat for boreal species, such as black spruce (Online Resource 1a), tamarack (Online Resource 8a) and trembling aspen (Online Resource 9a). Losses of projected climate habitat are pronounced at the southern fringe of the boreal forest, and the dry boreal forest regions in the eastern rain shadow of the Canadian Rocky Mountains. These losses of suitable realized climate niche space are consistently predicted with high certainty, regardless of the climate change scenario. Although yellow cedar and western hemlock are predicted to lose suitable climate habitat at their southern coastal range limits (Online Resource 10 and 15), habitat of coastal species appears to be generally well maintained at the species level. Habitat projections based on observed climate trends, represented by the 1997–2006 decadal average, are generally in the direction and magnitude of climate change predictions. Especially at higher latitudes, habitat projections based on observed climate trends appear to be approaching or exceeding those expected for the 2020s, for example black spruce (Online Resource 1a), aspen (Online Resource 9a), or white spruce (Online Resource 14a).

3.3 Elevation versus latitudinal shifts

Habitat projections for individual species populations are summarized by broad geographic regions (Table 3), and we report latitudinal and elevation shifts further aggregated over all 18 climate change scenarios. An important observation is that elevation and latitude shifts predicted by climate envelope modeling are not independent over multiple populations or
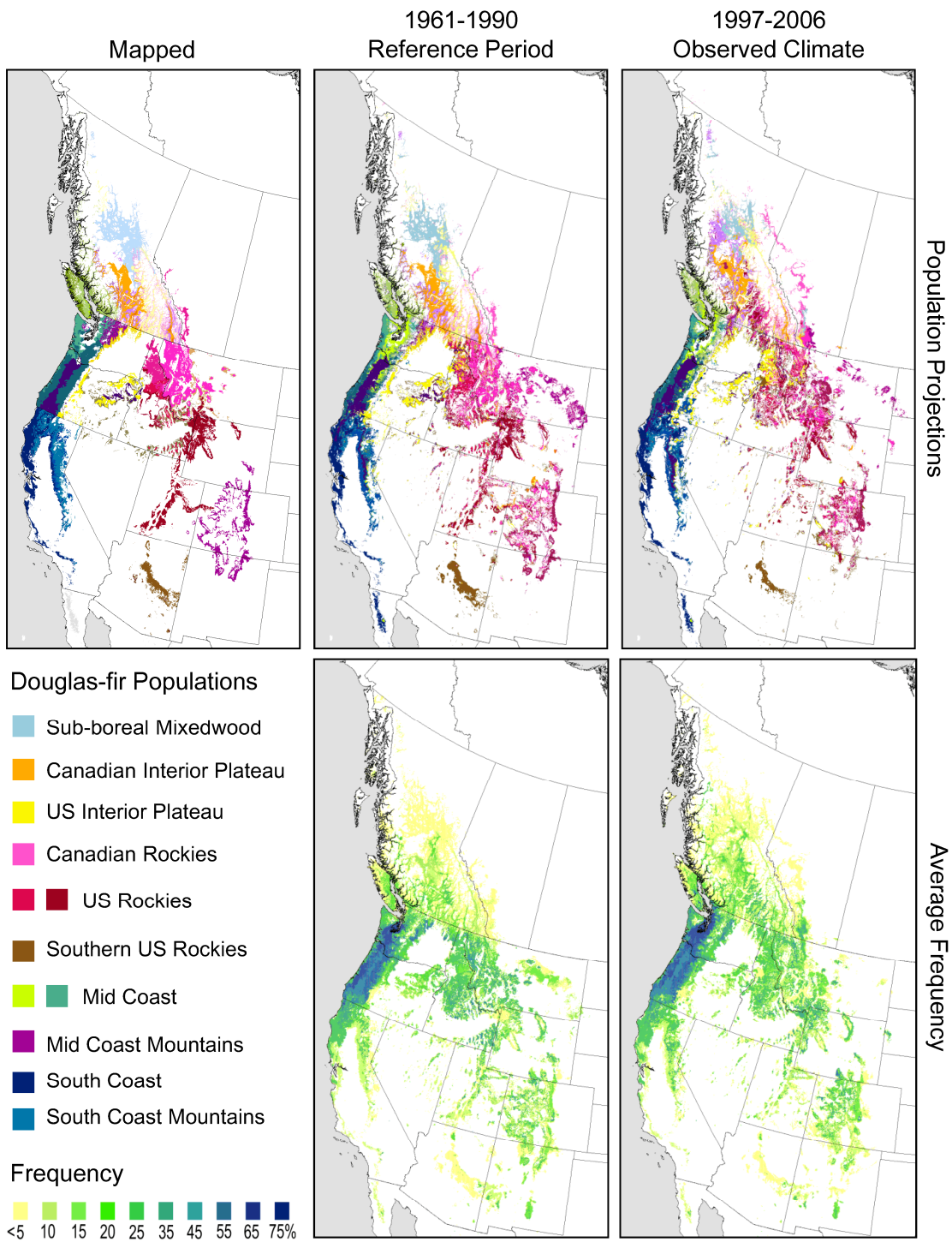
Fig. 1 Projections of Douglas-fir habitat for the 1961–1990 reference period and under recent climate change 1997–2006. The first rows of maps show projections of individual populations. In the second row, ecosystem modeling units were replaced with known species frequencies

multiple model runs. For example, an approximate climate match to a current population may in the future be found at higher elevation and the same latitude, at the same elevation but higher latitude, or through a combination of northward and upward shifts. This leads to a strong negative correlation between predicted elevation and predicted latitudinal shifts for particular species–region combinations, represented by symbols in Fig. 3.

## Projections for 18 General Circulation Models
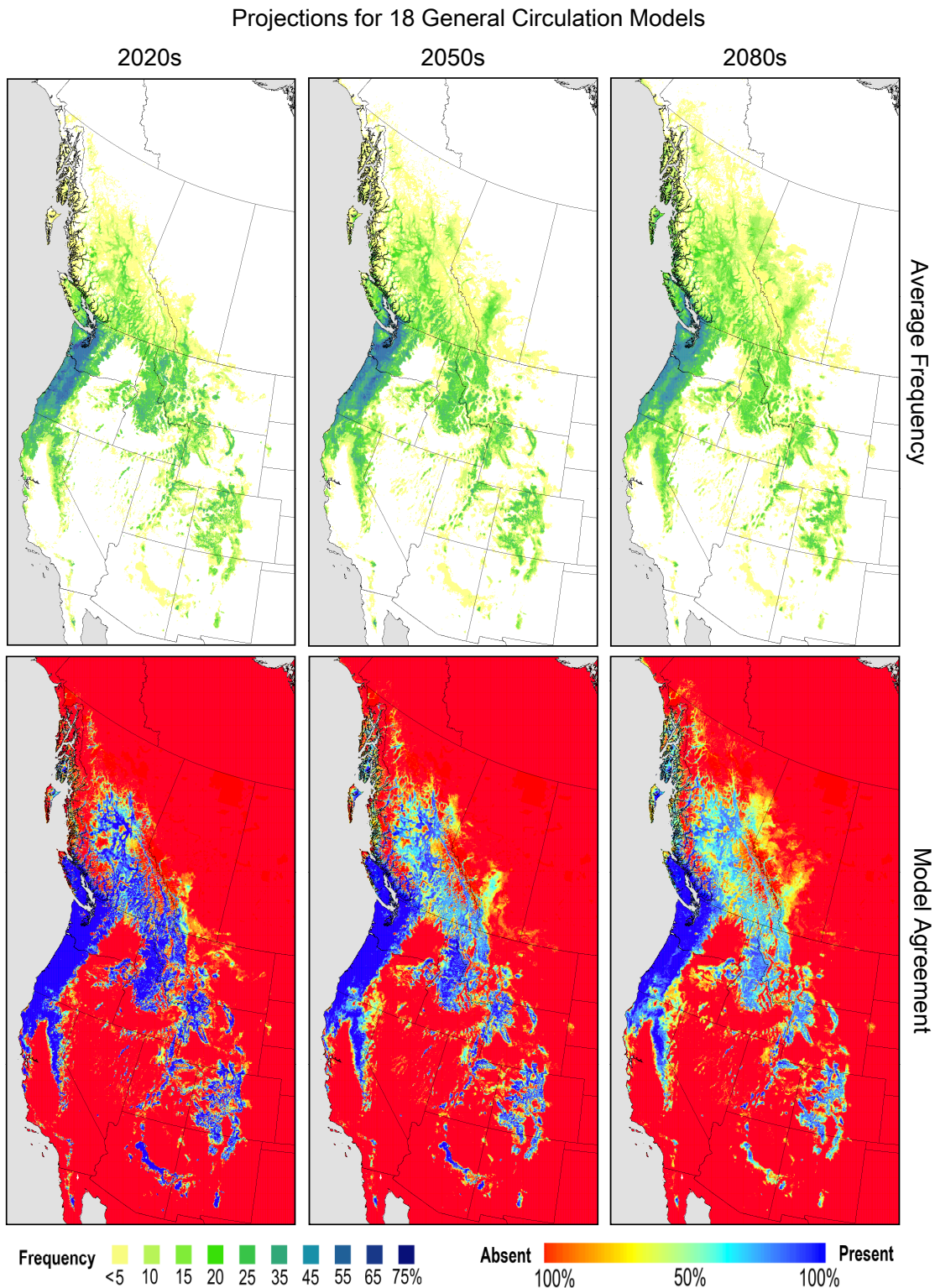
Fig. 2 Projections of Douglas-fir habitat for under climate scenarios for the 2020s, 2050s and 2080s. In the first row, ecosystem modeling units were replaced with known species frequencies. The second row shows the degree of consensus among projections based on multiple climate change scenarios

This relationship shown in Fig. 3 for the consensus projections of multiple populations holds true for individual model runs. Although similar climate change scenarios may produce rather different combinations of elevation and latitude shifts for individual

Table 3 The geographic regions that we use to summarize shifts in suitable habitat are defined by four ecological classification systems. The table lists the "zone" name for BC (Meidinger and Pojar 1991), the "natural subregion" name for AB (NRC 2006), the "ecoregion" name for SK and MB (Selby and Santry 1996), or the "level III natural region" name for the US (EPA 2007)

Region	Ecosystem polygons
North Coast	BC: Coastal Western Hemlock and Mountain Hemlock north of 51° latitude; US: Alaskan Panhandle
Mid Coast	BC: Coastal Western Hemlock, Coastal Douglas-Fir and Mountain Hemlock south of 51° latitude; US: Coast Range and Puget Lowlands
South Coast	US: Southern and Central California Chaparral and Oak Woodlands
North Coast Mountains	BC: Engelmann Spruce-Subalpine Fir and Interior Cedar-Hemlock north of 51° latitude.
Mid Coast Mountains	BC: Engelmann Spruce-Subalpine Fir, Interior Douglas-Fir, Mountain Spruce south of 51° latitude; US: Cascades and North Cascades
South Coast Mountains	US: Klamath Mountains, Southern California Mountains, Sierra Nevada
Canadian Rockies	BC: Engelmann Spruce-Subalpine Fir, Interior Cedar-Hemlock, Interior Douglas-Fir, Mountain Spruce and Sub-boreal Spruce within the mountain range; AB: Alpine, Subalpine, Montane and Upper Foothills
US Rockies	US: Northern Rockies, Idaho Batholiths, Middle Rockies,Canadian Rockies, Wasatch and Uinta Mountains, and Southern Rockies within mountain range
Boreal	BC: Boreal White and Black Spruce; AB: Athabasca Plain, Boreal Sub-arctic, Northern Mixedwood, Central Mixedwood, Dry Mixedwood, Kazan Uplands, Lower Boreal Hills and Peace-Athabasca Delta; SK/MB: Athabasca Plain, Churchill River Upland, Mid-boreal Upland, Mid-boreal Lowland and Boreal Transition
Sub-boreal Mixedwood	BC: Sub-Boreal Spruce, Sub-Boreal Pine-Spruce and Spruce-Willow-Birch
Canadian Interior Plateau	BC: Ponderosa Pine and adjacent Interior Douglas-Fir
US Interior Plateau	US: dry conifer forest occurring in selected parts of the Blue Mountains, Middle Rockies, North Cascades, and Eastern Cascades Slopes and Foothills
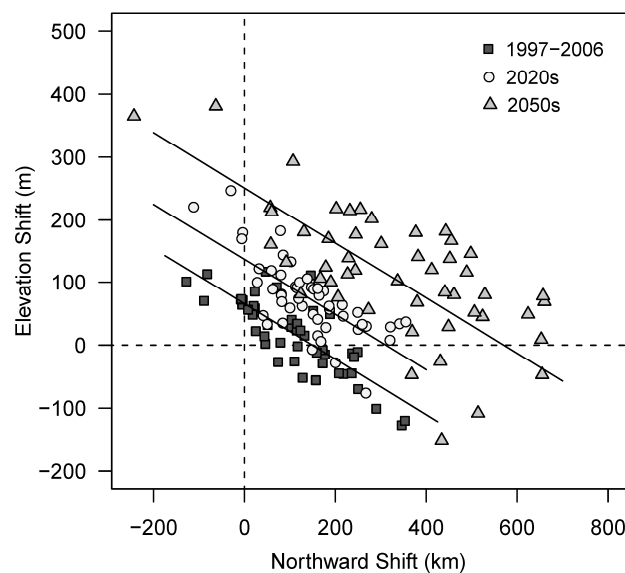
Fig. 3 Plot of the projected northward shift verses the shift in mean elevation for all populations of all species listed in Table 4. A linear regression trend line representing the overall trend δ Elevation=δ Latitude×0.44 is also provided for each period

ecosystem units (data not shown), elevation and latitudinal shifts can consistently be described by the formula: δ Elevation=δ Latitude×0.44. In other words, a 100 km north shift in latitude with the elevation held constant is equivalent to a 44 m upward shift in elevation with the latitude held constant. The standard error estimate for the slope of this relationship (0.44) is 0.06. The linear relationship explains 37, 54, and 56 % of the total variance in the predicted elevation versus northward shifts for the 1997–2006, 2020s and 2050s climates, respectively. Based on this formula we report the average elevation shift given a zero latitudinal change, and the average latitudinal shift, given a zero elevation change (Table 4).

3.4 Tracking habitat of populations

Under 1997–2006 climate conditions, representing an approximately 25-year climate change relative to the 1961–1990 reference period, climate habitat of populations across western North America has shifted on average 130 km north or approximately 60 m up in elevation. The largest habitat shifts due to observed climate trends were identified for the boreal and the Canadian and US Interior Plateau regions. This reflects warming trends of approximately +1.5 °C or more in mean annual temperature for these regions, and a reduction of mean annual precipitation by up to 20 % for the 1997–2006 average relative to the 1961–1990 reference period (data not shown).

Projected latitudinal or elevation shifts for western North America on average double for the 2020s (310 km north, 140 m elevation), and double again for the 2050s (590 km north, 260 m elevation) compared to habitat shifts calculated for the 1997–2006 observed climate (Fig. 3). As observed in the recent past, the most prominent shifts for the 2020s are predicted for the boreal and the US and Canadian Rockies regions. This primarily affects climate habitat for populations of black spruce, white spruce, aspen, and tamarack. For the 2050s northern and coastal populations of tree species are also projected to experience large geographic lags. For example, populations of yellow cedar, Sitka spruce, pacific silver fir, western hemlock and western redcedar would be affected (Table 4).

To provide a measure of variability of projections given in this table, average standard deviations across all populations for northward shifts are 123 km for the 2020s and 249 km for the 2050s. Average standard deviations for elevation shifts are 54 and 110 m for the 2020s and 2050s, respectively. Standard deviations for the 2080s are very large at the population level and even at the species level (Fig. 1 and Online Resources 1d–15d).

4 Discussion

4.1 Characteristics of the ecosystem-based modeling approach

Rather than just informing where habitat is lost, maintained, or gained at the species level, our modeling approach provides geographically referenced matches between current populations and matching climate conditions under climate change. Under the assumption that populations are indeed adapted to local climate conditions (e.g. Gray et al 2011), our projections suggest that northern and high elevation populations may be as vulnerable to climate change as populations at the trailing edge of the species range. Our analysis supports empirical data by Chen et al. (2010), and confirms reservations by Hampe (2004) on the correct interpretation of species distribution model projections.

Table 4 Northward and elevation shift of suitable habitat for populations relative to the 1961–1990 reference projection, averaged over 18 climate change scenarios. We report elevation change for a constant latitude, and latitudinal change for a constant elevation. For seed transfer these values represent maximum limits for a latitudinal *or* elevation transfer

Species	Region	1997–2006 shifts		2020s shifts		2050s shifts	
		North (km)	Elevation (m)	North (km)	Elevation (m)	North (km)	Elevation (m)
Black spruce	Boreal	223	98	439	193	834	367
	Canadian Rockies	106	46	317	140	642	283
	Sub-boreal Mixedwood	143	63	329	145	704	310
Douglas-fir	Canadian Interior Plateau	399	176	287	126	482	212
	Canadian Rockies	133	58	345	152	668	294
	Mid Coast	141	62	242	106	535	235
	Mid Coast Mountains	88	39	164	72	417	183
	South Coast	75	33	380	167	544	239
	Sub-boreal Mixedwood	161	71	348	153	424	317
	US Interior Plateau	193	85	133	58	721	39
	US Rockies	175	77	240	106	407	179
Engelmann spruce	Canadian Rockies	62	27	344	151	719	317
	Mid Coast Mountains	31	14	195	86	399	176
	US Interior Plateau	51	22	404	178	557	245
	US Rockies	299	132	264	116	379	167
Lodgepole pine	Boreal	166	73	337	148	709	312
	Canadian Rockies	62	27	322	142	633	278
	Mid Coast Mountains	113	50	260	114	571	251
	Sub-boreal Mixedwood	75	33	380	167	544	239
	US Interior Plateau	154	68	264	116	786	202
	US Rockies	168	74	309	136	542	238
Pacific silver fir	Mid Coast	175	77	267	118	544	239
	North Coast	215	95	323	142	739	325
Ponderosa pine	US Interior Plateau	102	45	392	172	586	258
	US Rockies	231	102	278	122	533	294
Sitka spruce	Mid Coast	75	33	95	42	268	118
	North Coast	157	69	354	156	834	367
Tamarack	Boreal	114	50	337	148	675	297
	Canadian Rockies	10	4	366	161	549	242
Trembling aspen	Boreal	197	87	387	170	735	323
	Canadian Rockies	81	36	334	147	624	275
	Sub-boreal Mixedwood	192	84	360	158	514	226
	US Interior Plateau	130	57	133	58	765	39
	US Rockies	92	40	137	60	372	164
Western hemlock	Canadian Rockies	281	124	411	181	772	339
	Mid Coast	135	59	182	80	417	184
	North Coast	159	70	366	161	856	377
Western larch	Canadian Rockies	170	75	404	178	648	285
	US Rockies	196	86	532	234	803	353

Table 4 (continued)

Species	Region	1997–2006 shifts		2020s shifts		2050s shifts	
		North (km)	Elevation (m)	North (km)	Elevation (m)	North (km)	Elevation (m)
Western redcedar	Canadian Rockies	274	121	379	167	697	307
	Mid Coast	155	68	254	112	568	250
	North Coast	128	56	328	145	753	331
Western white pine	Canadian Rockies	314	138	496	218	749	329
	Mid Coast Mountains	12	5	147	65	392	172
White spruce	Boreal	207	91	419	184	817	359
	Canadian Rockies	57	25	307	135	627	276
	Sub-boreal Mixedwood	106	47	356	157	685	301
Yellow cedar	Mid Coast	70	31	262	115	515	227
	North Coast	153	68	371	163	830	365

Compared to other species distribution models, our ecosystem-based approach appears to yield similar levels of predictive accuracy (e.g. Schroeder et al. 2010; Roberts and Hamann 2012). We find the best accuracy for coastal species with AUC values above 0.9, which is generally interpreted as excellent predictive accuracy. Almost identical AUC values were obtained in semi-independent cross-validations (Roberts and Hamann 2012) and the approach yielded fair accuracy in truly independent regional and palaeoecological validations (0.78 and 0.75, respectively). A notable difference to standard species distribution models is that error rates in our ecosystem-based modeling approach are driven by omission error (e.g. Rehfeldt et al. 2009). From a management perspective, determining species choice for management applications should therefore be quite safe because we tend to underpredict rather than overpredict suitable habitat.

4.2 Adaptational lag implies a need for assisted migration

Our results suggest that climate change observed over the last 25 years has already resulted in a notable lag of populations relative to their 1961–1990 climate niches. These lags are in the same direction and approximately half of the magnitude as in climate change predictions for the 2020s (Table 4, Fig. 3). Our analysis implies that seed could be moved 130 km north or 60 m up in elevation, although the values vary for different species and different regions in western North America. Notably, this recommendation relies on a number of assumptions that we discuss in more detail in the following paragraphs.

Standard reforestation practice in western North America relies on seedzone delineations to restrict seed movement from collection locations to panting sites, sometimes in combination with transfer limits expressed in geographic or elevation distances (e.g. Ying and Yanchuk 2006; Hamann et al 2011). These rules are based on the assumption that populations are broadly adapted due to high gene flow (e.g. Morgenstern 1996). As a consequence, current planting stock recommendations are made for broad macro-climatic regions, represented by ecosystem or seedzone delineations (Hamann et al 2011; Ying and Yanchuk 2006). In contrast, there are no seed collections or breeding programs that provide especially adapted genotypes for particular soil conditions or topographic positions. Instead, foresters

choose appropriate species for various micro-site conditions, soils, or topographic positions, guided by handbooks for local site classifications.

Our modeling approach accounts for current reforestation practices by using the same or similar ecosystem delineations as modeling units, that also serve to restrict seed transfer in current reforestation practice. We further make similar foundational assumptions: Optimality of local populations refers to the same concept as equilibrium assumptions in species distributions modeling, and seed zones are often approximated with the help of ecosystem delineations even when genetic data from provenance trials is available (Hamann et al. 2011). Therefore, violation of these assumptions has similar consequences in projections as in current reforestation programs. For example, local optimality does not always apply, compromising the potential maximum productivity of current plantations (Matyas 1990). Our future projections would simply perpetuate any adaptational lag and sub-optimal productivity that pre-existed during the 1961–1990 reference period.

We should further note that in the modeling approach we use, soil and topographic variables matter in determining the realized niche, even though we do not use these variables as predictors. Hence, local silvicultural prescriptions need to be transferred along with species populations. For example, if a species currently occurs only on deep, nutrient rich soils in a particular ecosystem or seedzone, and a forester considers a climate-based seed transfer according to Table 4, then the target sites further north or higher in elevation should also have deep, nutrient rich soils. The projections of Table 4, like current seed zones, offer guidance as to which planting stock is best for a broad climatic region. Species selection for specific planting sites still remains an important responsibility of forest managers.

4.3 Uncertainty requires short-term adaptation strategies

Even though the life span of most tree species included in this study exceeds the 2080s, we think that forest resource managers need to focus on the immediate future when developing seed transfer prescriptions for a number of reasons. First, uncertainty in habitat projections for the 2020s are moderate, but they dramatically increase towards the 2080s (Fig. 2, Online Resources 1–15). Secondly, since trees are most vulnerable to climatic factors at the seedling stage (Black and Bliss 1980; Donovan et al. 1988), we could not currently plant genotypes that would be optimally adapted to 2080s climate. Third, long-distance transfers far outside the current species range implied by 2080s projections may lead to issues not considered by the model (e.g. required mycorrhizal associations, or changes to day length regimes that control the species' phenology). Therefore, seed transfers according to the 1997–2006 and 2020s projections will have the best chance of success. Although we realize that this will mean that tree populations will continue to lag behind their optimal climate, targeting current and 2020s climate conditions is still a low-risk improvement over status-quo management practices that essentially target climate conditions of the past century.

Another compelling argument to locally change status-quo management practices are the substantial number of observed climate change impacts on forest heath and productivity (e.g. Allen et al. 2010; Barber et al. 2000; McDowell et al. 2010; Michaelian et al. 2010; Peng et al. 2011). Such additional sources of information allow forest practitioners to weigh the risk of changing existing practices against the risk of status-quo management, exemplified in a case study for aspen by Gray et al (2011). Although the link between changing climate conditions and ecological impacts can be quite complex (e.g. Hennon et al. 2006; Woods et al. 2005), we think that these observations in combination with climatic habitat projections are a compelling argument for testing different species or different genotypes that may be better adapted to new climatic realities.

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