Bioclimate Models and Change Projections to Inform Forest Adaptation in Southwestern Colorado: Interim Report

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Cooperators: Bureau of Land Management, Tres Rios Field Office (BLM)
Mesa Verde National Park (MVNP)
Southern Ute Indian Tribe (SUIT)
San Juan National Forest (SJNF)
Rio Grande National Forest (RGNF)
Grand Mesa, Uncompahgre, and Gunnison National Forests (GMUG)
Rocky Mountain Research Station
Colorado Natural Heritage Program
Mountain Studies Institute
Western Wildland Environmental Threat Assessment Center

Abstract. This analysis quantifies the topoclimate niche of 14 tree species in southwestern Colorado and predicts the 2060 niche distribution for each species. It draws on comprehensive, high-resolution vegetation datasets, a precise climate downscaling model, GCMs and RCPs used by IPCC, a foremost decision-tree learning algorithm, and advanced analytical techniques. The models accurately predict recent species distributions at high resolution based on reference climate, slope, and aspect. The results are presented as spatially explicit change zones to enhance utility in management. Results can be used to: (a) determine site-specifically the most appropriate management actions for climate adaptation of vegetation, (b) focus efforts where they have the greatest likelihood of long-term success, and (c) identify potential climate refugia.

Introduction

In the southern Rocky Mountains, it is increasingly evident that weather, insects, diseases, stand conditions, and fire will interact to transform forests as the climate changes. We have already seen widespread changes. Fires have been larger and more severe (van Mantgem *et al.* 2013, Westerling *et al.* 2006). Piñon ips responded to the turn-of-the-century drought by killing piñon on over 2.9 million acres in the 4-corner states (Breshears *et al.* 2005). In Colorado, sudden aspen decline impacted 1.2 million acres (17% of the aspen cover type) (Worrall *et al.* 2015), mountain pine beetle killed trees on 3.4 million acres, and spruce beetle has impacted 1.6 million acres to date (Howell *et al.* 2016). These agents kill stressed trees, often building their populations to kill trees in the absence of stress.

These large-scale disturbances provide a strong reminder of the powerful influence of climate on vegetation. The Forest Service and other agencies increasingly mandate extensive consideration of climate change in project, landscape, and forest planning. While vulnerability assessments and other elements provide a good overview of potential climate change impacts and general adaptation measures, they do not provide the quantitative, spatially explicit projections needed to adapt vegetation management to climate change. Impacts to tree species will vary greatly across the landscape – from habitat lost to new habitat emerging. Our management today should be quite different among these locations.

Bioclimate models offer an approach to develop spatially explicit projections of climate change impacts. By analyzing the relationship between known presence/absence of a species and reference climate (which led to the current distribution) at each point, they can predict the likelihood that a given climate will be suitable. Predicted distributions based on grids of reference climate match very well with known distributions. Grids of projected future climate then result in spatially explicit projections of future suitability. Bioclimate models have been extensively used and tested in research (Fettig *et al.* 2013, Gray & Hamann 2012, Hamann & Wang 2006, Iverson *et al.* 2008, Rehfeldt *et al.* 2006, Rehfeldt *et al.* 2014a, Sáenz-Romero *et al.* 2012, Worrall *et al.* 2013). Their application in management has been limited due to the coarse scale of mapping (~ 1 km resolution), lack of topographical response, and the complexity of results. Recent work has addressed these issues: methods for mapping at a 90-meter pixel scale suitable for landscape analysis, incorporation of topographic variables to increase fine-scale accuracy, and a method for projecting change zones that are directly applicable to management (Rehfeldt *et al.* 2015).

Here we report the methods, results, and some management implications of bioclimate modeling and change projections for 14 tree species in southwestern Colorado. The objectives of this phase of the project were to: (a) develop bioclimate models for dominant tree species of southwestern Colorado based on local data, incorporating topographic variables, and with results presented at a scale useful to management, and; (b) interpret the models by projecting change zones for the species (Lost, Threatened, Persistent, and Emergent) to make them useful for management.

Methods

Models were developed for 14 tree species (Table 1). The process for model development and projection can be summarized as follows for a given species. The steps are described in more detail below.

1. Assemble and process 'training' data
    a. Points of known presence and absence of the species
    b. Reference climate, slope, and aspect for each point
2. Provide training data to the 'Random Forests' algorithm. The algorithm determines the combination of topoclimate variables and values that are importantly associated with presence and absence of the species.
3. Mapping
    a. Create rasters of reference and projected future climate variables for the study area.
    b. Run the variables for each raster cell through the model, obtaining votes among all the 'trees' for presence or absence in that cell. The result is a map of votes, indicating suitability, for each climate.
4. To project change from the reference period to the future, compare the vote grids for the two climates.

Table 1. Species used in bioclimate modelling.

Species	**Common name**	**Code**
Abies concolor	white fir	ABCO
Abies lasiocarpa	subalpine fir (including corkbark)	ABLA
Juniperus osteosperma	Utah juniper	JUOS
Juniperus scopulorum	Rocky Mountain juniper	JUSC2
Picea engelmannii	Engelmann spruce	PIEN
Picea pungens	blue spruce	PIPU
Pinus aristata	bristlecone pine	PIAR
Pinus concolor	lodgepole pine	PICO
Pinus edulis	piñon	PIED
Pinus flexilis	limber pine	PIFL2
Pinus ponderosa	ponderosa pine	PIPO
Populus tremuloides	trembling aspen	POTR5
Pseudotsuga menziesii	Douglas-fir	PSME
Quercus gambelii	Gambel oak	QUGA

Study area

Our study area 'window' is bounded by longitudes -109.1, -105.3 and latitudes 36.9, 39.45. This is just outside Colorado's borders with Utah and New Mexico, reaching just north of the GMUG and east to include the Sangre de Cristo Mountains (Figure 1).

Software

All analyses and data manipulations were conducted in R (R Core Team 2016). Within R, we primarily used the packages **rgdal** (Bivand *et al.* 2015) for working with spatial polygons and points and their attributes, **raster** (Hijmans 2015) for working with rasters and certain other geographic data, **randomForest** (Liaw & Wiener 2002) for building and using Random Forests models, **yaImpute** (Crookston & Finley 2007) for building prediction rasters, and **ggplot2** (Wickham 2009) for graphing and mapping. Many other packages were used at various steps.

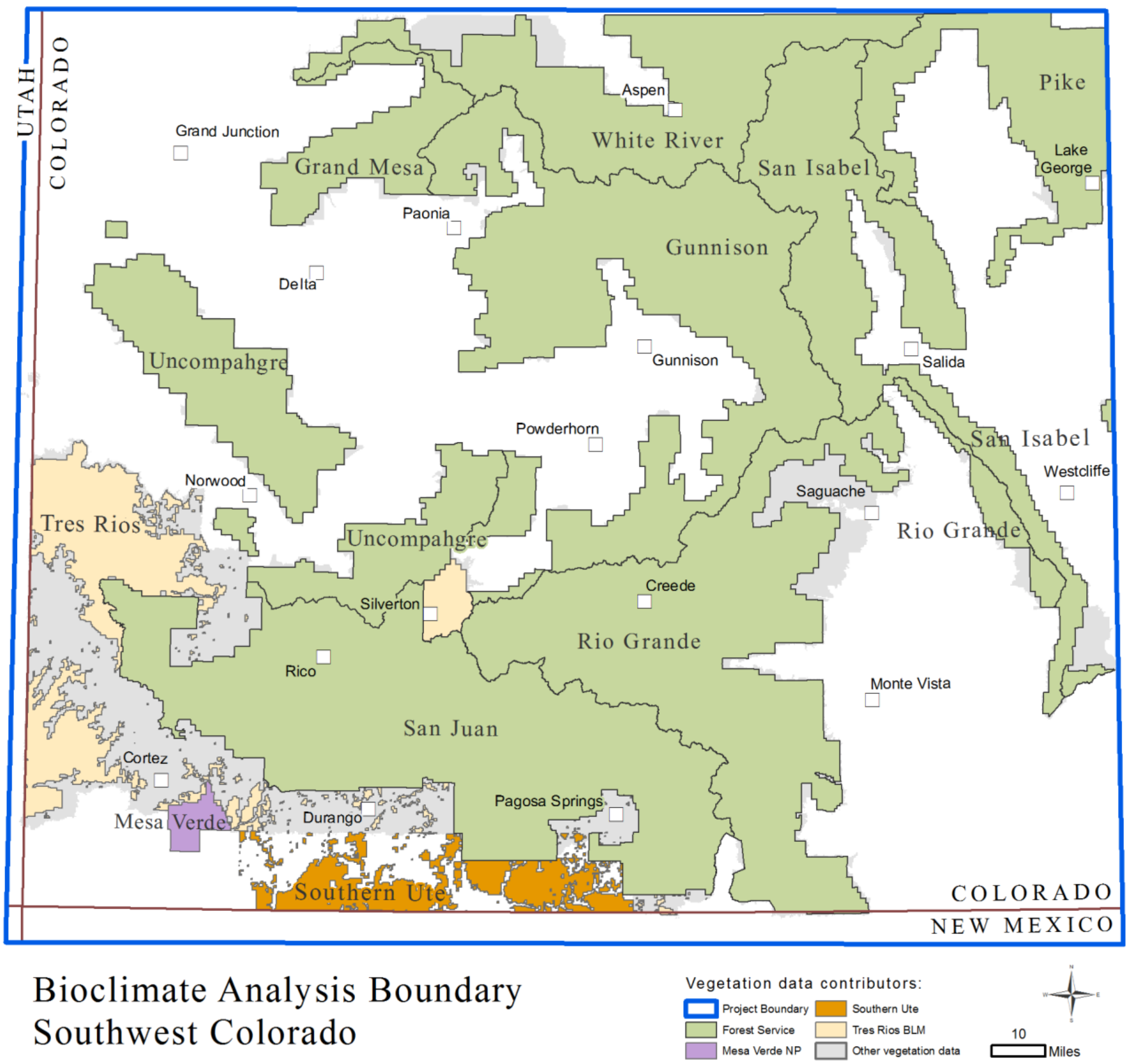
Training data

Spatial vegetation data were obtained from the land management units listed above (under Cooperators). These represent the highest resolution data available. They are based on expert analysis and interpretation of remote images and ground observations, not on vegetation models. They were supplemented by Forest Inventory and Analysis (FIA) plots.

National Forest System

For national forest data (including Tres Rios BLM, whose data are maintained together with SJNF), we used data from a nationwide USvegNRIS geodatabase compiled in 2015. We searched the NRIS_VegSubpopulations table for species codes in the field SPECIES_SYMBOL that are used to indicate presence of each species. If any were present, the species was considered present in the associated polygon; otherwise, it was considered absent. We found no species data in the few polygons of the Carson NF inside our window. In the few polygons of the Manti-La Sal NF, most had species codes in the field SUBGROUP_1, so those were used to indicate presence/absence.

Figure 1. Map of window used for modeling, bounded by longitudes -109.1, -105.3 and latitudes 36.9, 39.45.



Several corrections or refinements were made. The floor of the San Luis Valley, not part of the Rio Grande NF, contained very large polygons (> 30,000 acres). Most of them had no vegetation data; one had several tree species represented although most of the polygon was treeless. Those polygons were deleted.

On the GMUG, 78 polygons around Ouray known to have white fir were set to 'present' for that species, although white fir was not represented in the vegetation data.

Lodgepole pine that occurs in the Uncompahgre, San Juan, and southern Rio Grande NFs is all comprised of plantations outside of the native range. In the shapefile, we set lodgepole pine to 'absent' in these areas, west of longitude -107.4 OR south of latitude 37.7.

On the SJNF, white and subalpine fir were confused during automated analysis of satellite imagery to populate the vegetation data. The result was that white fir appears to exist much higher in elevation than it does, all the way to the Continental Divide. To correct this, we waited until we had a grid of sample points because elevation was associated with each point (see below). On the SJNF, for any points above 3000 m (9843 ft) and containing ABCO in the vegetation attributes, we set ABLA as present. This added 746 new ABLA points. For any points meeting the same criteria, we then set ABCO to absent. This resulted in dropping 12,853 ABCO points.

Southern Ute Indian Tribe

SUIT data are recorded as forest types. After discussing with foresters representing the tribe and Bureau of Indian Affairs, we created a table of presence/absence rules for each species in each forest type. Species whose presence in a type was variable were assigned 'NA' for that type. When building models for a given species, any sample points showing "NA" for that species were first deleted.

Mesa Verde National Park

Similar to SUIT, MVNP data is recorded as vegetation types. We used the most specific, the Base_Class field, and developed rules for each type as with SUIT. For polygons in developed areas, we assigned NA for any species that occurred anywhere in the Park.

Large burned areas in the Park were marked as 'post-fire', and the pre-existing vegetation was not indicated. However, the best data for our purposes are the vegetation that grew there recently, even if it is currently absent. Therefore, MVNP provided supplemental files including a 1996 vegetation shapefile, together with data from 147 vegetation plots in the Park. We used the post-fire polygons from the main shapefile to clip the 1996 shapefile. The 1996 polygons and associated vegetation attributes were used to replace the burned polygons in the main shapefile.

To take advantage of the plot data, we extracted the presence of tree species noted in each plot. Because the plot is a small part of the polygon in many cases, we decided not to use plot data to assign absence; only presence. Using the plot coordinates, we identified the polygon containing each plot, and assigned the corresponding presence data to each polygon. If the polygon already had presence for a species based on shapefile attributes, it was unchanged.

Sample points

All resulting shapefiles, containing presence-absence data for each species, were sampled with a grid of points. On SUIT and MVNP, we used a grid interval of 0.0023 degrees (Table 2). On NFS/BLM land, because of the large area, we used a slightly larger interval, 0.0025 degrees. Each point was assigned presence-absence data of the polygon over which it fell. This process assured sampling proportional to area and covered the topography thoroughly. The final count of sample points from vegetation shapefiles was 840,069, distributed among units as shown in Table 3.

FIA plots

Sample points from spatial vegetation data were supplemented with data from FIA plots (O'Connell *et al.* 2015). As a supplement, FIA plots are attractive because they offer accurate species identification and complete census on about 0.17 acre (subplots were lumped in each plot). Also, they occur on all land ownerships. In addition, outside our window, they provide access to vegetation data for climates that do not currently occur in the window, but are projected to occur in the future.

Table 2. Distance between points in sample grids in the center of the study area.

	0.0023 degrees	**0.0025 degrees**
Latitude	255.3 m	277.5 m
Longitude	201.5 m	219.1 m

Table 3. Number of vegetation sample grid points in each unit.

Management unit	**Number of points**
Grand Mesa NF	25,372
Gunnison NF	122,873
Uncompahgre NF	75,031
Manti-La Sal NF	167
Pike NF	48,305
Rio Grande NF	147,376
San Isabel NF	67,581
San Juan NF and Tres Rios BLM	252,779
White River NF	71,656
Mesa Verde National Park	5,728
Southern Ute Indian Tribe	23,201
TOTAL	840,069

We retrieved complete FIA plot records for 6 states (AZ, CA, CO, NM, NV, UT) in August and September 2015. We eliminated any plot sample records before 2002 and any plots with PLOT_STATUS 3 (not sampled, may or may not have forest). We eliminated duplicate plot records so each plot was represented only once. We dropped plots that had any condition 4 (census water). To focus on the southwestern desert climates, in Nevada, we dropped plots north of latitude 38.5; in California, we dropped plots west of longitude -118.3.

We then compared the provided elevation of the true location with the 90-meter DEM elevation (Jarvis *et al.* 2008) of the public (fuzzed/swapped) location. We removed plots with more than 50 m discrepancy, on the assumption that those were fuzzed or swapped to a greater distance. All remaining plots inside our study area window were kept and used as training data.

In preliminary trials, piñon and some junipers appeared to expand in suitability and becoming emergent at lower elevations than where they currently occur. We determined that the future climates in these areas do not occur to any extent in the window in the reference period. If no procedures are available to account for novel climates (Rehfeldt *et al.* 2012), RF is forced to extrapolate into climates it has not been trained for. After obtaining reference climate data for each FIA plot (see 'Reference climate data' below), we filtered the remaining outside plots to retain only those that had climates similar to future climates in Four Corners and San Luis Valley areas.

We accessed the FIA TREE tables to assemble species presence/absence records for each plot. FIA staff provided DEM slope and aspect for true locations of each plot (before fuzzing/swapping). The final count was 7280 FIA plots: 2633 inside the window and 4647 outside. All FIA plots were placed in the pool of points to be sampled as training data. However, to ensure all outside plots were used in every training sample, any not picked randomly were added before model development (see Model Development below).

Desert grid

Portions of the Four Corners and San Luis Valley, where no trees existed, were not adequately sampled in the management units or FIA plots. Therefore, we delineated treeless polygons in them (verified with satellite imagery) and established a grid of 7493 points. All were assigned 'absent' for all tree species.

Reference climate data and variables

The coordinates of each point and its 90-m DEM elevation (Jarvis *et al.* 2008) were submitted to a server that provides climate data (Crookston & Rehfeldt 2008) based on the spline climate model described by Rehfeldt (2006). For each point, we retrieved climate variables derived from monthly averages for the reference period 1961-1990. Additional 'transformed' variables were calculated from derived variables. For model development and prediction, we used a total of 23 variables (Table 4). We assigned slope and aspect to each point (for calculation of heatload) from 90-meter DEMs as noted above. 'heatload' is a replacement for the Cartesian slope/aspect variables used previously (Rehfeldt *et al.* 2015). It more effectively reflects the influence of topography on local climate. It was the second most important variable in predicting presence, and makes fine-scale mapping more accurate. We use the term "topoclimate" to refer to the climate together with the influence of slope and aspect.

In summary, there were 854,842 points available for training the models, including 840,069 from spatial vegetation datasets, 7280 FIA plots, and 7493 from the supplemental desert grid. Any points that had 'NA' for presence of the species at hand were deleted prior to sampling for model building.

Model Development

Our approach to model development was to apply a well-established protocol (Joyce & Rehfeldt 2013, Ledig *et al.* 2010, Rehfeldt *et al.* 2006, Rehfeldt & Jaquish 2010, Rehfeldt *et al.* 2015, Worrall *et al.* 2013) adapted slightly to take advantage of our extensive vegetation data. These procedures use the Random Forests classification algorithm (Breiman 2001) as implemented in the randomForest package of R (Liaw & Wiener 2002, R Core Team 2016). This algorithm constructs 'forests' of decision 'trees'. Given ample training data with true presence/absence, Random Forests is the preferred algorithm because it is unexcelled in accuracy, it runs efficiently with very large datasets, and it generates a sound, unbiased, internal estimate of goodness of fit (Biau & Scornet 2016, Breiman 2001, Cutler *et al.* 2007, Liaw & Wiener 2002, Prasad *et al.* 2006). Because each tree is constructed with a different subset of the data and each node is split using one of a random subset of the predictor variables, while the decision is made by the ensemble, it is robust against overfitting. Disadvantages in some cases include: (a) it is demanding in terms of training data, which should be ample and must include presence and absence observations; (b) there is a learning curve to program it (no graphical interface); (c) advanced techniques may be required to optimize the training dataset and prediction accuracy, and; (d) the model is difficult to interpret ecologically without additional analysis.

Table 4. Derived and transformed variables used in model development.

	Derived variables (calculated by server from monthly values)
mat	mean annual temperature
map	mean annual precipitation
gsp	growing season precipitation, April to September
mmin	mean minimum temperature in the coldest month
mmax	mean maximum temperature in the warmest month
fday	Julian date of the first freezing date of autumn
ffp	length of the frost-free period (days)
dd5	degree-days > 5 C (based on mean monthly temperature)
d100	Julian date the sum of degree-days > 5 C reaches 100
dd0	degree-days < 0 C (based on mean monthly temperature) ≈ winter cold
mmindd0	degree-days < 0 C (based on mean minimum monthly temperature)
winp	winter precipitation: (Nov+Dec+Jan+Feb)
	Transformed variables (calculated from derived variables)
pratio	precipitation ratio, growing season to annual: gsp/map
adi	annual dryness index: $dd5^{0.5}$/map
sdi	summer dryness index: $gsdd5^{0.5}$/gsp
adimindd0	adi*mmindd0
sdimindd0	sdi*mmindd0
dd0map	dd0/map
gspdd5	gsp * dd5 / 1000
mapdd5	(map*dd5)/1000
tdiff	mtwm-mtcm (temperature difference between warmest and coldest month)
heatload	0.339 + 0.808*cos(L)*cos(S) + -0.196*sin(L)*sin(S) + -0.482 * cos(A) *sin(S), where L=latitude in radians, S=slope in radians, A=aspect folded around NE/SW in radians; from McCune and Keon (2002)
mapheat	map/heatload

The protocol we follow uses multiple 'forests' to model the climate niche. A unique training dataset is built for each forest. Random Forests is most effective when there are approximately equal observations within the classes, that is, in our case, about equal numbers of presence and absence observations. Constructing training datasets from presence-absence databases such as ours ordinarily requires sampling observations, because (a) there invariably are disproportionate numbers of observations in the presence-absence classes, and (b) computer resources often limit the size of the training data that can be run by the Random Forests algorithm. In our case, presence observations range from only 2% to 36% of the total (Table 5). Previous modeling has shown that maintaining presence observations no less than 40% of the training dataset adequately satisfies Breiman's conditions of equality among classes. We chose 42% as the threshold to compensate for the samples that were later forced into dataset, which were mostly absence observations. Our computing limits turned out to be about 300,000 observations. Previous research has also shown that a doubling of presence observations in the training dataset greatly reduces errors of omission while exposing the model to an increased number of absence observations. These three contingencies govern the sampling protocol.

Table 5. Number and types of observations in the full training dataset for each species and in samples allocated to forests.

		Observations (percent of total)				Samples in forest (percent of total)		
Species	Total obser-vations (n)	Present	Absent, in envelope	Absent, outside envelope	Total samples per forest (n)	Present	Absent, in envelope	Absent, outside envelope
ABCO	848,331	4.0	68.5	27.6	159,938	42.0	42.0	16.0
ABLA	854,842	21.5	71.9	6.7	300,000	42.0	52.5	5.5
JUOS	834,977	8.0	69.1	22.9	300,000	42.0	44.7	13.3
JUSC2	834,977	3.5	85.9	10.6	138,257	42.0	50.6	7.4
PIAR	854,842	3.7	88.5	7.8	152,071	42.0	51.9	6.1
PICO	854,842	8.2	73.6	18.1	300,000	42.0	46.8	11.2
PIED	849,302	13.3	82.1	4.6	300,000	42.0	53.6	4.4
PIEN	854,842	35.6	60.9	3.5	300,000	42.0	54.1	3.9
PIFL2	854,842	2.3	91.8	5.9	92,743	42.0	52.9	5.1
PIPO	854,278	17.2	80.9	1.9	300,000	42.0	54.9	3.1
PIPU	854,357	1.8	93.2	5.0	71,662	42.0	53.4	4.6
POTR5	847,481	35.1	63.0	1.9	300,000	42.0	55.0	3.0
PSME	848,485	16.8	81.1	2.1	300,000	42.0	54.9	3.1
QUGA	843,153	17.6	80.0	2.5	300,000	42.0	54.7	3.3

To build training datasets, we used the following rules to govern the selection of presence observations such that their total would be about 42% of the number in the dataset. If presence observations were >42% of 300,000, that is, >126,000, presence samples were randomly chosen (ABLA, PIEN, PIPO, POTR5, PSME, QUGA, Table 5). If presence samples were <42% of the training data total yet >63,000, duplicate observations were chosen at random to fulfill the 42% threshold (JUOS, PICO, PIED). If presence samples were <63,000, then all observations were added twice to the training data, which then required reducing the size of the dataset in order to maintain presence at 42% (ABCO, JUSC2, PIAR, PIFL2, PIPU). After completion, the total number of observations in the training data sets ranged from 71,662 to 300,000. In all cases, presence observations were represented at 42% of the total (Table 5).

To allocate absence observations to the training datasets, the protocol assorts absence observations into two groups depending on their climatic similarity with species distributions. This is done to concentrate in the training data observations that would be most difficult to separate from presence observations. To this end, an n-dimension climatic envelope (sensu Box *et al.* 1999) is made to bound the climatic limits of distribution of a species; each dimension of the envelope is delimited in climate space. To reduce the dimensions of the envelope, we conducted a principle components analysis to produce orthogonal vectors of linear combinations of the climate variables. Because strong intercorrelations exist within the matrix of climate variables, we limited the number of climate variables entering into the analysis to an array for which intercorrelations were $r<0.9$: map, mmin, dd5, dd0, adi, adimindd0, sdimindd0, and pratio. The first 3 principal components accounted for 99% of the variance and were used to define the envelope. The protocol also calls for each dimension of the envelope to be enlarged somewhat; we expanded each vector by ±0.1 standard deviation. Absence observations within the expanded envelope were considered 'in' the envelope; otherwise 'out'. Those observations classified as 'in' are the most difficult to separate from presence.

Because 42% of each training set is presence observations, we allocate 58% to absence observations, favoring those from the 'in' group. However, because the proportion of 'in' and 'out' groups varied so widely, we scaled the number of absence observations from the two groups according to the proportion of the total number of 'out' observations to the total number of observations in the database. When the proportion was high, the 'in' sample approached 42% of the training dataset; when the proportion was low, the 'in' sample approached 55% of the training dataset (Table 5). As a result, the 'in' group comprised 42-55% of the training data, or 73-95% of each absence sample.

After drawing training data accordingly, the forced samples (FIA plots outside the window) were examined to see if any were already in the sample, and the remainder was added.

The number of forests used for each species-specific model was determined by the ratio of the total number of absence points in the envelope to the number that were put in the training data, constrained between 8 and 30. In this way, the probability was high that each absence observation would be used at least once. Each forest was comprised of 100 trees.

Random Forests was run in a stepwise fashion, first eliminating the four poorest predictors (based on decrease in accuracy when it was removed), then 3, then 2, and then one at a time until only one variable remained. Based on out-of-bag error rates (see below, Model verification – goodness of fit), a reasonably parsimonious number of variables to keep in the final model was determined to be eight.

When the resulting model is used for prediction, an observation is run down all trees in all forests. Each tree then casts a vote as to whether the topoclimate of that observation would be suited to the species.

Model verification – goodness of fit

Maps of topoclimate niche and species distribution

We 'predict' current distribution of a species' topoclimate niche using rasters of reference climate variables. These are based on the same reference climate dataset as the point data used for training (Crookston & Rehfeldt 2008). We input a raster of elevation with the extent of our window, and receive a corresponding raster for each derived variable. We add slope and aspect from 90-m rasters and calculate heatload and other transformed variables for each raster cell. The model reads all the variables, one cell at a time, and outputs votes for suitability at each cell. We can compare the resulting raster of votes with distribution based on spatial vegetation data where that is available.

Quantitative

Goodness of fit between model predictions and actual observations can be evaluated with errors of commission (predicting presence for a point where the data indicate absence) and errors of omission (predicting absence where the data indicate presence). Errors of commission are calculated as the number of absence points erroneously predicted as presence, divided by the total number of absence points. Likewise, errors of omission are calculated as the number of presence points erroneously predicted to be absent, divided by total number of presence points. Total error rate is total number of errors divided by total number of points tested.

Error is reported in two ways. Both ways use, in part or in whole, data not used to build the model. Both assume that the vegetation data used for training and testing are without error. The first method was 'out-of-bag' errors. When each tree is built, about one third of the training dataset provided to its forest is randomly withheld internally by Random Forests and not used to build that tree (i.e., not in the 'bag'). The algorithm then puts each out-of-bag sample down its respective tree to get predictions and calculate error. We report here those errors averaged among all forests.

The second error rate reported is the entire training dataset (up to 854,842 points) tested against all forests. Each forest was developed using some subset of these samples, but never all. A voting threshold of 50% was used to predict presence or absence for an observation.

Projecting future suitability

We used variable grids for future climates to make projections. The future climates we used are for the decade 2055-2064 (hereafter referred to as 2060) using three representative general circulation models (GCMs) used by the International Panel on Climate Change (IPCC). GCM output was obtained from CMIP AR5 (http://cmip-pcmdi.llnl.gov/cmip5/) for CCSM4 from the Community Earth System http://www.cesm.ucar.edu/models/ccsm4.0/), GFDLCM3 from the Geophysical Fluid Dynamics Laboratory (http://www.gfdl.noaa.gov/coupled-physical-model-cm3), and HadGEM2ES from the Met Office, UK (http://www.metoffice.gov.uk/research/modelling-systems/unified-model/climate-models/hadgem2). Representative carbon pathways were used to represent three scenarios for greenhouse gas emissions (Van Vuuren *et al.* 2011). We used RCP4.5, RCP6.0 and RCP8.5; the RCP2.6 scenario was ignored because assumptions of reduced emissions already are invalid. Climate variable grids for the resulting 9 climates were used as input for the models. The resulting 9 vote grids were then averaged to make an average projection of future climate suitability for each cell (referred to as CGH, an acronym for the three GCMs used).

Change classes

Because management approaches will vary based on anticipated changes in the topoclimate niche, it is helpful to classify species' habitat geographically according to the potential severity of the impact, that is, the change in votes. Management can then be tailored to these classes. We used the difference in model output between the reference and future periods to classify change zones as shown in Table 6.

Table 6. Change classes based on comparing reference vs. future suitability for a species.

Change classes	**Reference votes**	**2060 votes**	**Interpretation**
LOST	≥ 0.5	< 0.3	future climate will be so unfavorable, the species is unlikely to survive the century
THREATENED	≥ 0.5	0.3-0.5	future climate will be unfavorable, but may survive if resilient
PERSISTENT	≥ 0.5	≥ 0.5	future climate will remain suitable
EMERGENT	< 0.5	≥ 0.5	areas outside current distribution that will become climatically suitable

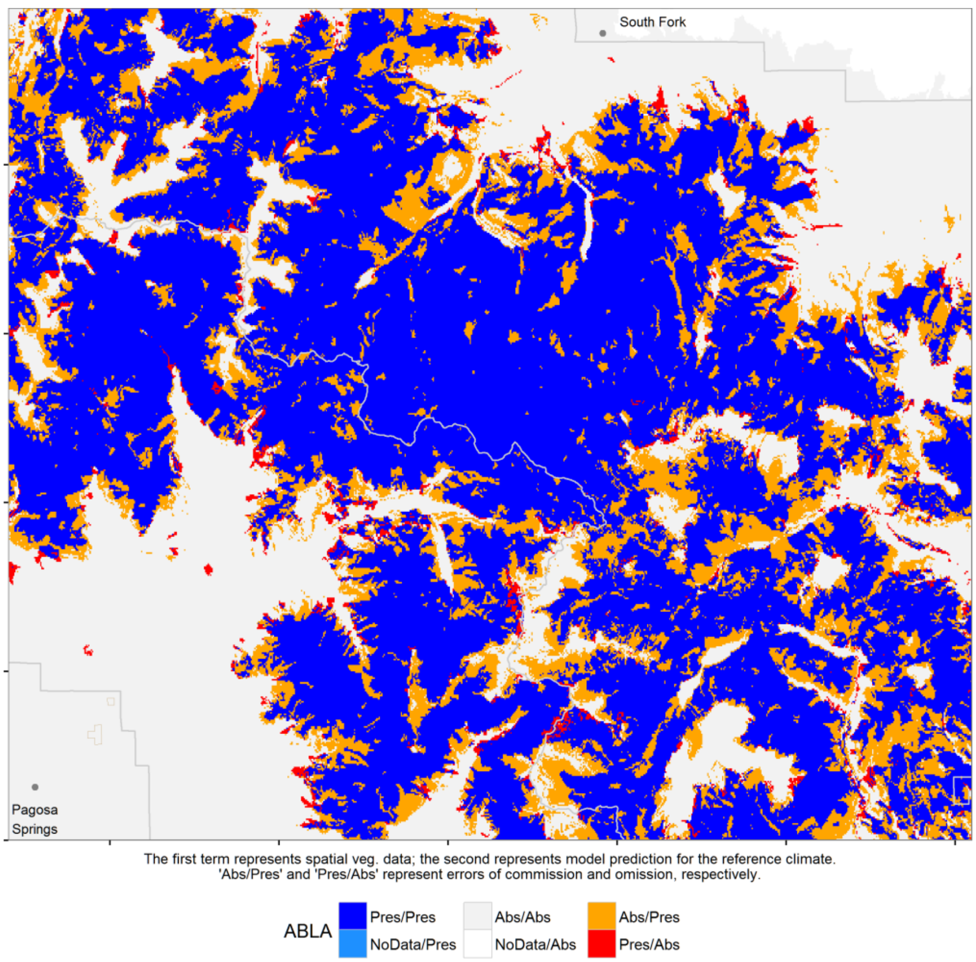
Results and Discussion

Goodness of fit

Since they are based on real presence/absence data, there is a sound method for estimating fit of Random Forests models. Predictions for the reference period can be compared to actual presence-absence data. In this case, goodness of fit can be examined visually and quantitatively.

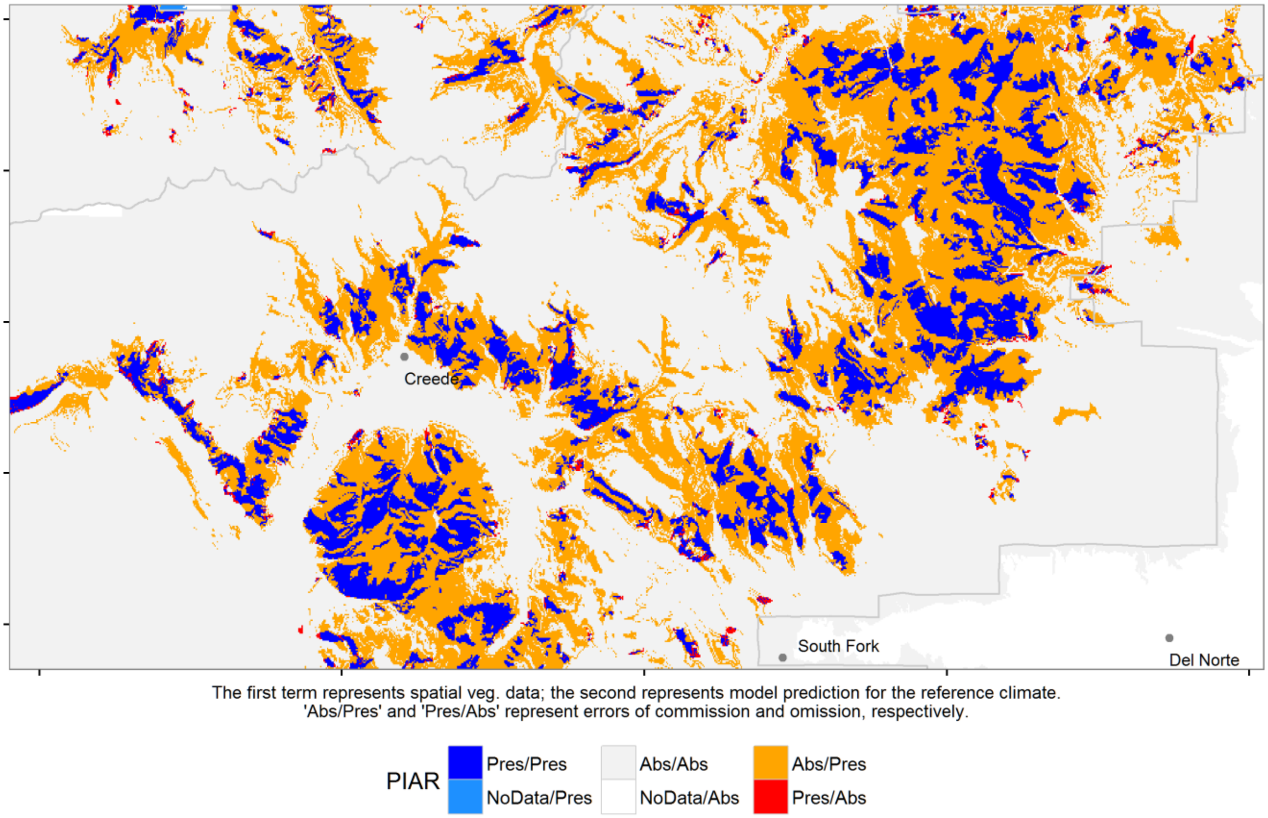
Visual comparisons (Figure 2) illustrate the accuracy of the models in representing the distribution of the species. Errors of omission (red), the most serious kind of error, are few and generally near the fringes of the distribution. Apparent errors of commission (orange) tend to be scattered through the distribution in small patches. These errors are almost all within areas correctly predicted to be suitable (dark blue).

Figure 2. Mapped model predictions based on reference climate compared to presence based on spatial vegetation data, for subalpine fir on the RGNF and SJNF in the area around Wolf Creek Pass.



Some less common species have more extensive orange areas (apparent errors of commission, Figure 3). Even in these cases, however, the model correctly predicts general areas where the species occurs. Also, errors of omission remain infrequent.

Figure 3. As in Fig. 1, but bristlecone pine in the area around the La Garita Mountains on the southeastern GMUG and northern RGNF.



It must be remembered that the models do not predict distribution, they predict suitable topoclimate niche. It is quite possible for the model to correctly predict suitability for an area that does not have the species. Apparent errors of commission may represent:

1. **Unoccupied niche**. The models may well be correct in many cases that the climate and topography are suitable for the species, but it is not there. Often this is due to disturbance history, succession, poor substrate, or dispersal limitations.
2. **Inaccurate vegetation data**. On the national forests, most of the vegetation data was populated through interpretation of aerial photographs or processing of satellite imagery. Uncommon species may be missed and misidentifications may exist.
3. **Model error**. Some portion of the 'errors of commission' is due to actual model error.

To the extent these apparent errors of commission are indeed model errors, it means that the model is somewhat overly optimistic in predicting suitable habitat. In turn, this means we are somewhat conservative in projecting lost habitat in the future. This is important because all habitat for these 5-needle pines is projected to be lost.

Quantitatively, model predictions for Engelmann spruce and aspen fit actual observations at least as well as those from a previously published study using these two species on the GMUG (Rehfeldt *et al.* 2015). Except for the other abundant species (subalpine fir, Douglas-fir), fit for other species was considerably better (Table 7).

Table 7. Goodness of fit for bioclimate models. 'Out-of-bag' errors are based on testing with samples provided to random forests during model fitting but withheld internally for independent error testing. 'All samples' represents the entire presence-absence dataset tested against all forests. Based on voting threshold of 50% to predict presence.

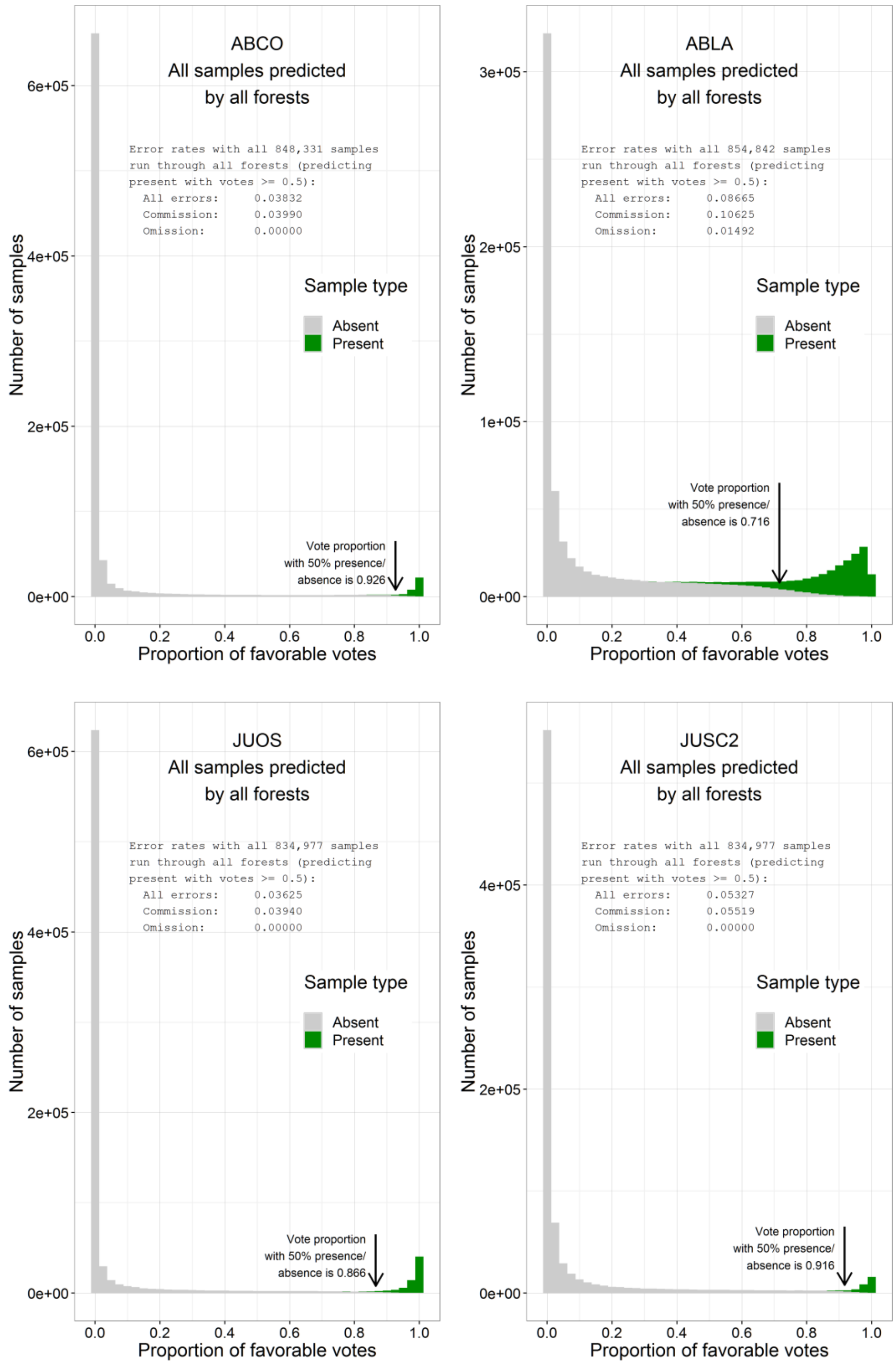
	Out-of-bag errors (%)				All-sample errors (%)		
Species	Commission	Omission	Total		Commission	Omission	Total
ABCO	4.2	0.0	2.5		4.0	0.0	3.8
ABLA	14.2	13.5	13.9		10.6	1.5	8.7
JUOS	4.8	0.6	3.1		3.9	0.0	3.6
JUSC2	5.7	0.1	3.4		5.5	0.0	5.3
PIAR	7.3	0.0	4.3		7.1	0.0	6.8
PICO	5.8	0.7	3.7		4.8	0.0	4.4
PIED	7.5	6.3	7.0		6.1	0.0	5.3
PIEN	13.0	13.7	13.3		8.8	5.4	7.6
PIFL2	6.2	0.1	3.7		6.4	0.0	6.3
PIPO	9.0	8.1	8.6		7.5	0.3	6.2
PIPU	6.9	0.1	4.2		7.3	0.0	7.2
POTR5	15.5	18.5	16.8		9.5	7.1	8.6
PSME	14.0	14.8	14.3		10.7	0.3	9.0
QUGA	8.7	7.0	8.0		7.3	0.3	6.0

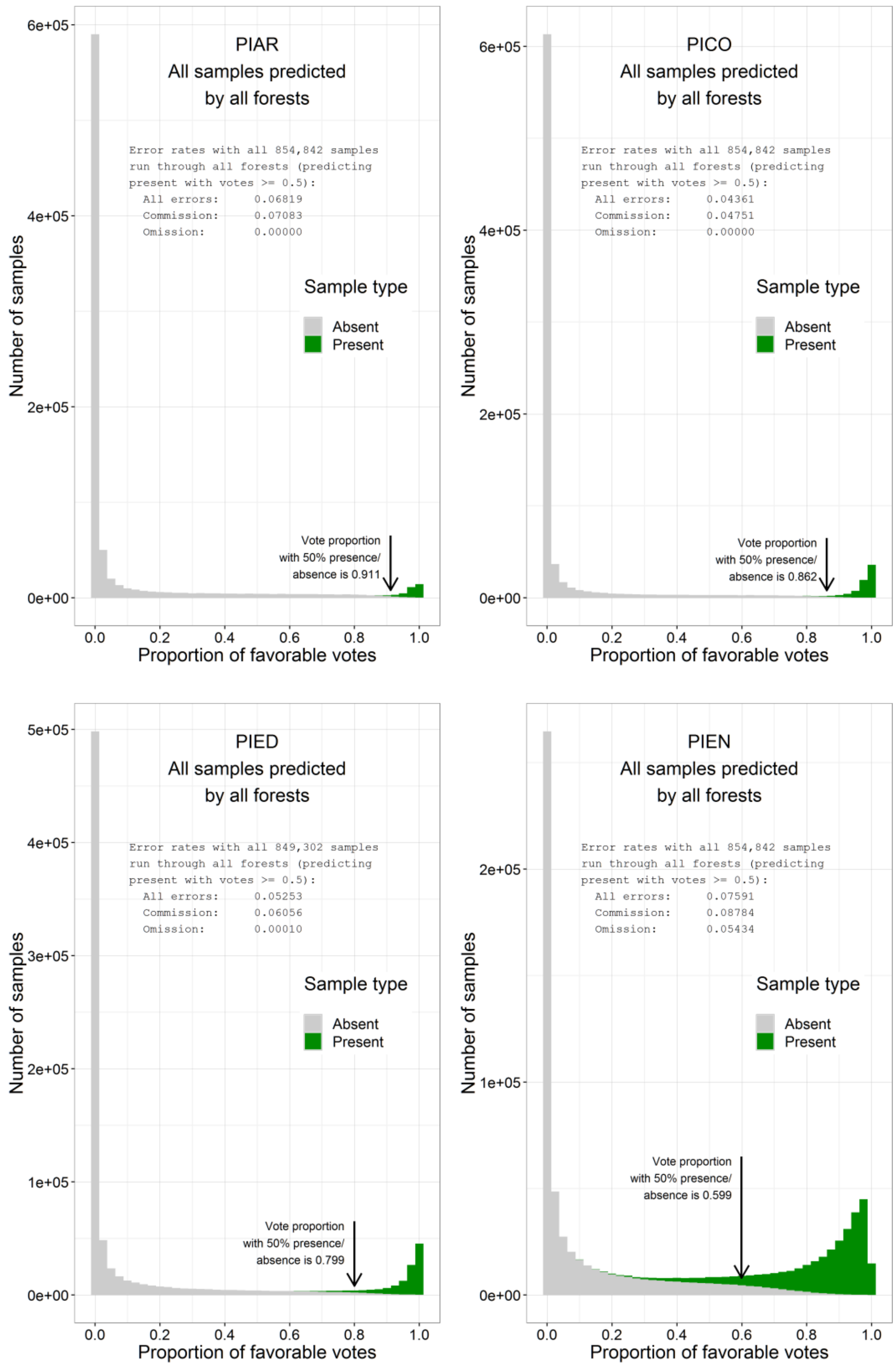
Except for the most common species, errors of omission were generally much fewer than errors of commission. When all samples were tested against all forests, they are all in single digits and generally quite close to 0. Errors of commission, on the other hand, were generally higher.

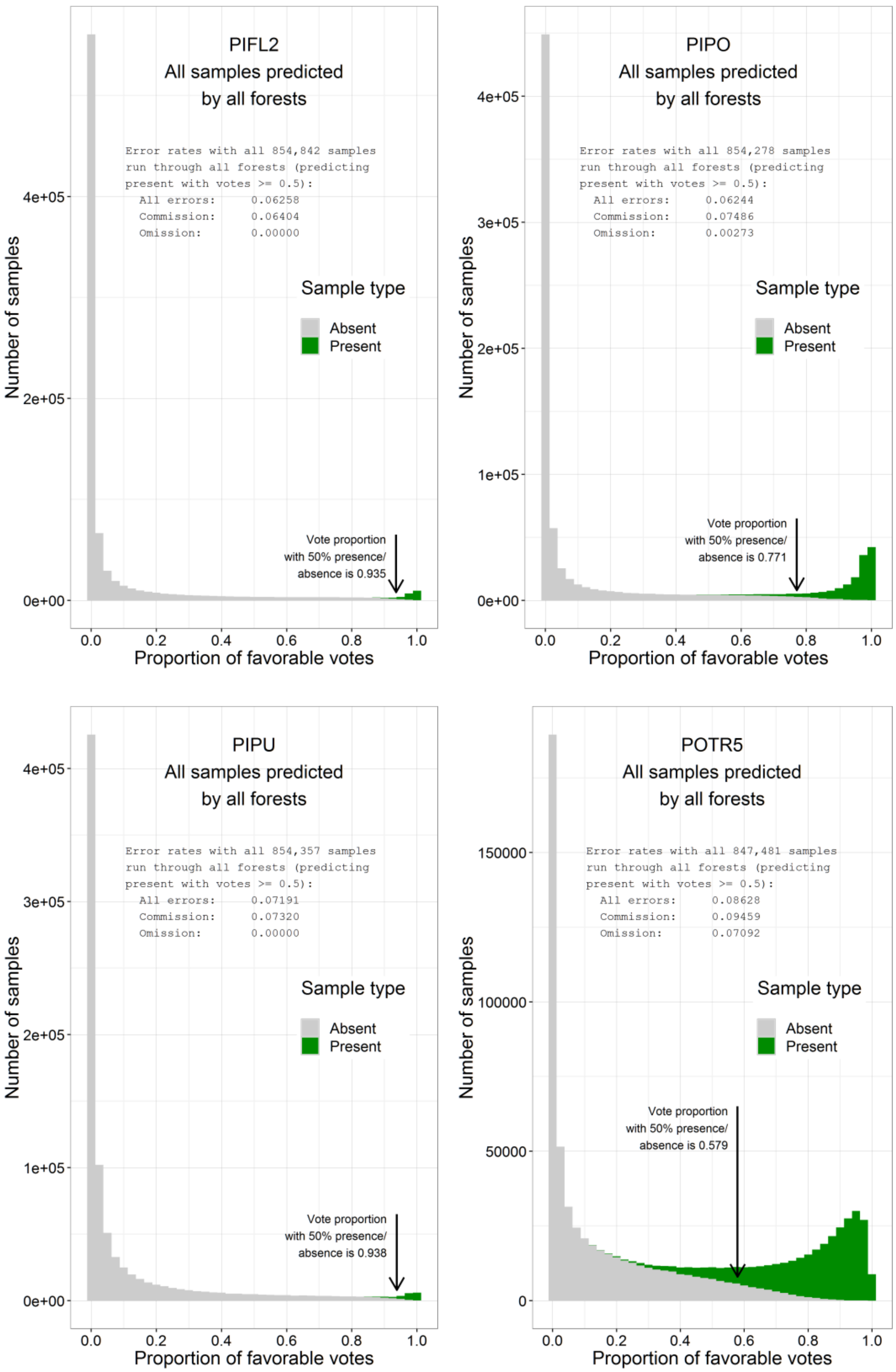
In general, out-of-bag errors are higher than those for the entire dataset. There are several reasons for this. First, absence samples provided during model development, including out-of-bag samples were selected as being the most difficult to distinguish from presence. This is justified from the view that errors of omission are much more informative than errors of commission because there are many valid ecological reasons that a species does not occur in all places where the topoclimate alone is suitable. Second, none of the out-of-bag samples were used for model development in the forest where they were tested.

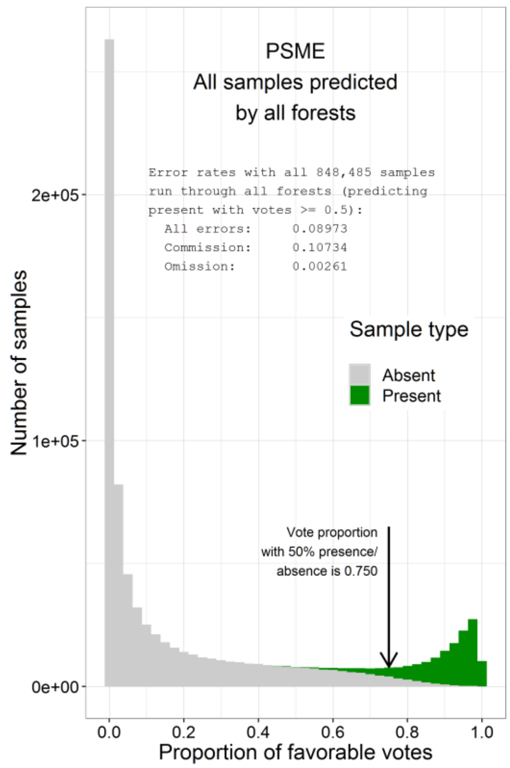
More detailed information about model performance and errors can be gleaned from histograms of the frequency of vote proportions (Figure 4). Vote proportions near 0, all trees voting no, are most abundant, and contain no samples with the species present. As favorable vote proportions increase, the proportion of samples with the species eventually starts to increase. Where vote proportions are near 1, all trees voting yes, all samples have the species. The vote proportion is marked with an arrow where there is an equal number of sample points of actual presence and absence.

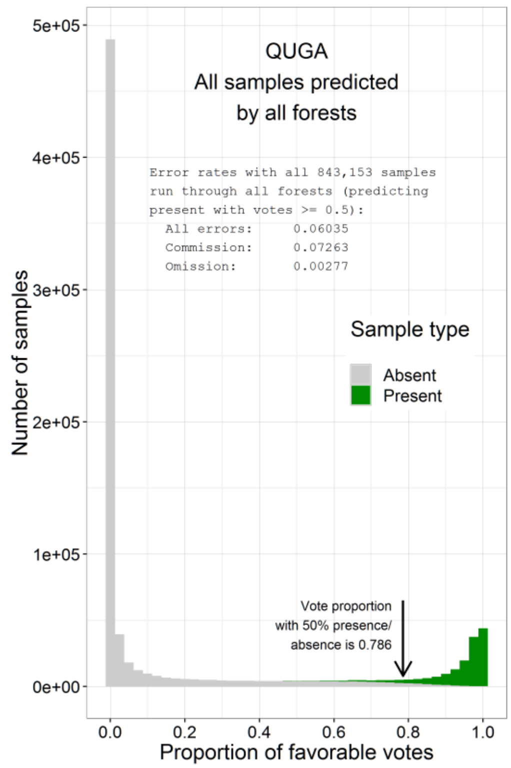
Figure 4. Histograms of vote proportion by sample type (absent or present).




PIAR
All samples predicted
by all forests
Error rates with all 854,842 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.06819
Commission: 0.07083
Omission: 0.00000
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.911
Number of samples
Proportion of favorable votes
PICO
All samples predicted
by all forests
Error rates with all 854,842 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.04361
Commission: 0.04751
Omission: 0.00000
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.862
Number of samples
Proportion of favorable votes
PIED
All samples predicted
by all forests
Error rates with all 849,302 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.05253
Commission: 0.06056
Omission: 0.00010
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.799
Number of samples
Proportion of favorable votes
PIEN
All samples predicted
by all forests
Error rates with all 854,842 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.07591
Commission: 0.08784
Omission: 0.05434
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.599
Number of samples
Proportion of favorable votes


PIFL2
All samples predicted
by all forests
Error rates with all 854,842 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.06258
Commission: 0.06404
Omission: 0.00000
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.935
Number of samples
4e+05
2e+05
0e+00
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of favorable votes
PIPO
All samples predicted
by all forests
Error rates with all 854,278 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.06244
Commission: 0.07486
Omission: 0.00273
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.771
Number of samples
4e+05
3e+05
2e+05
1e+05
0e+00
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of favorable votes
PIPU
All samples predicted
by all forests
Error rates with all 854,357 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.07191
Commission: 0.07320
Omission: 0.00000
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.938
Number of samples
4e+05
3e+05
2e+05
1e+05
0e+00
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of favorable votes
POTR5
All samples predicted
by all forests
Error rates with all 847,481 samples
run through all forests (predicting
present with votes >= 0.5):
All errors: 0.08628
Commission: 0.09459
Omission: 0.07092
Sample type
Absent
Present
Vote proportion
with 50% presence/
absence is 0.579
Number of samples
150000
100000
50000
0
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of favorable votes





Variable importance

The order of elimination showed that variable importance varied among the species (Table 8). Collating the variable rankings (Table 9) showed that only two variables were among the top 8 for all species, pratio (ratio of growing season precipitation to annual precipitation, separating continental precipitation patterns from monsoonal) and heatload (a function of slope, aspect, and latitude related to the effect of insolation, illustrating the importance of topography in altering local climate).

Table 8. Order of removal of most important 14 variables during stepwise random forest fitting. The 8 variables in the final model are highlighted. Starting with 23 variables. See Table 4 for variable definitions.

ABCO	ABLA	JUOS	JUSC2	PIAR	PICO	PIED	PIEN	PIFL2	PIPO	PIPU	POTR5	PSME	QUGA
mmin	fday	map	mmindd0	mmindd0	ffp	d100	d100	mapheat	gspdd5	mapheat	d100	mmin	dd0map
winp	winp	gsp	d100	dd0map	mmax	mapheat	map	adimindd0	mapheat	adimindd0	mmindd0	winp	dd5
mmax	map	gspdd5	adimindd0	gspdd5	mapdd5	mmindd0	sdimindd0	mmindd0	ffp	winp	winp	mapheat	map
tdiff	gspdd5	dd0	ffp	ffp	winp	sdimindd0	winp	dd0map	map	mmindd0	mapdd5	mmindd0	mapheat
mmindd0	ffp	mapheat	gspdd5	tdiff	dd0map	gspdd5	gspdd5	dd5	dd0map	dd0	gsp	tdiff	sdimindd0
mapdd5	dd0map	tdiff	mmin	mapheat	adimindd0	winp	dd0map	ffp	sdimindd0	mapdd5	dd0map	adimindd0	ffp
sdimindd0	mapheat	mapdd5	tdiff	mapdd5	mapheat	dd0map	mapheat	gsp	winp	mmin	mapheat	gspdd5	dd0
adimindd0	sdimindd0	sdimindd0	dd0map	adimindd0	mmindd0	gsp	gsp	mmin	mmindd0	heatload	gspdd5	gsp	adimindd0
gspdd5	pratio	dd0map	sdimindd0	gsp	sdimindd0	mapdd5	mapdd5	gspdd5	adimindd0	sdimindd0	sdimindd0	dd0map	winp
ffp	mapdd5	winp	dd0	mmin	gsp	adimindd0	tdiff	heatload	heatload	dd0map	tdiff	mapdd5	tdiff
dd0	tdiff	adimindd0	pratio	heatload	heatload	tdiff	pratio	tdiff	gsp	pratio	heatload	sdimindd0	pratio
heatload	heatload	pratio	heatload	sdimindd0	pratio	pratio	adimindd0	sdimindd0	pratio	gspdd5	adimindd0	pratio	heatload
gsp	adimindd0	heatload	mapdd5	dd0	tdiff	heatload	heatload	dd0	mapdd5	gsp	pratio	heatload	gsp
pratio	dd0	mmindd0	gsp	pratio	gspdd5	dd0	dd0	pratio	tdiff	tdiff	dd0	dd0	mapdd5

The next most important variables were related to winter cold. dd0 (degree-days < 0 C) is closely related to mmindd0 and variables that represent interactions of dryness indices with winter cold (adimindd0, sdimindd0). tdiff (temperature difference between warmest and coldest month) reflects the degree that the climate is controlled by continental influences (or its antithesis, monsoonal influences). Growing-season precipitation was fifth overall.

In attempting to interpret how the variables influence presence, consider that the relationships are likely quite complex. Breimann (2001), who developed the methodology, referred to random forests as a "black box" and wrote that "A forest of trees is impenetrable as far as simple interpretations of its mechanism go." A simple relationship between a variable and likelihood of presence is unlikely. The variables interact, so that the effect of one depends on another. There may be peaks of effect somewhere along the range of values, threshold values, and inverse relationships at different parts of the range. The decision trees have tens of thousands of nodes (decision points). Furthermore, each tree was trained on a different subset of the data and thus has a different method of making predictions. Although it is possible to tease out relationships and examine decision trees, the process is very complex.

Table 9. Importance rankings of top 8 variables for each species (8 is most important) and for all species together (SUM); based on order of elimination.

	pratio	heatload	dd0	tdiff	gsp	mapdd5	adimindd0	sdimindd0	gspdd5	dd0map	mmindd0	winp	mmin	ffp	mapheat	SUM
ABCO	8	6	5		7		2	1	3					4		36
ABLA	3	6	8	5		4	7	2							1	36
JUOS	6	7				1	5	2		3	8	4				36
JUSC2	5	6	4	1	8	7		3		2						36
PIAR	8	5	7		3	1	2	6					4			36
PICO	6	5		7	4			3	8		2				1	36
PIED	6	7	8	5	2	3	4			1						36
PIEN	5	7	8	4	2	3	6								1	36
PIFL2	8	4	7	5	1			6	3				2			36
PIPO	6	4		8	5	7	3				2	1				36
PIPU	5	2		8	7			3	6	4			1			36
POTR5	7	5	8	4			6	3	2						1	36
PSME	6	7	8		2	4		5	1	3						36
QUGA	5	6	1	4	7	8	2					3				36
SUM	84	77	64	51	48	38	37	34	23	13	12	8	7	4	4	

Projections into the future

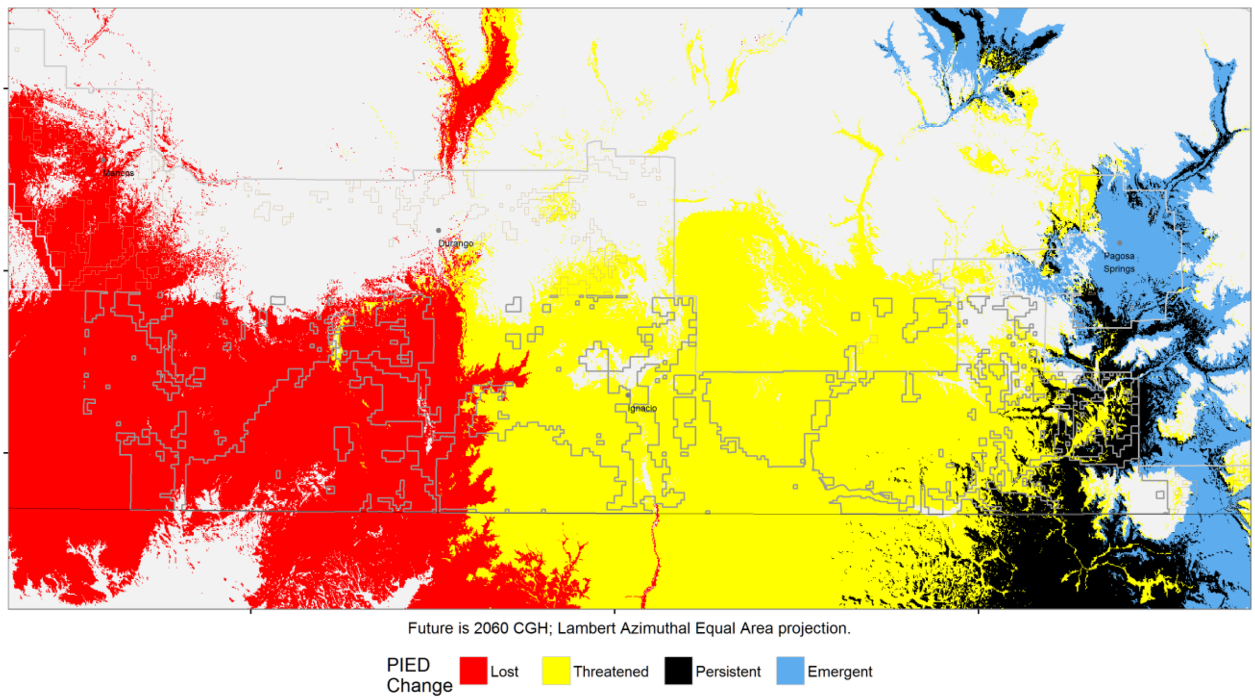
Projections of change zones for 2060 were based on cell-by-cell comparison of the vote raster for the reference period and the average vote raster from 9 future climate scenarios. Maps of change zones are provided separately. Because the study area is so large, maps are produced for various subsets of the area. Rasters can be provided on request for use in GIS. An example of a change map for PIED around the Southern Ute Indian Reservation illustrates how the change classes are distributed in zones (Figure 5).

The threatened class was included in order to be conservative when declaring habitat lost. A few of the most common species have a non-zero, but low, chance of species presence with votes < 0.5 (Figure 4).

Pessimistically, one could lump this category with lost, but the species is likely to persist longer here than in the lost zone.

The lost zones indicate that, by 2060, unsuitable climate may be widespread in the current habitat of most species (Table 10). Much habitat is also in the threatened class, where change in votes are equivocal, and there is less confidence in the habitat being either lost or persistent. For most species, potential new habitat in the emergent category offsets the losses to some extent, but future distributions are likely to be smaller (Table 10).

Figure 5. Distribution of change classes for piñon in the Southern Ute Indian Reservation.



The most severe losses are projected for the 5-needle pines (limber and bristlecone) and lodgepole pine. All current habitat is projected to be lost and no new habitat is expected to emerge. There is strong agreement for this outcome among projections based on individual climate scenarios. Blue spruce and white fir are similar, but there is some threatened habitat rather than all lost. Rocky Mountain juniper extends the pattern with more threatened, but still almost no persistent and little emergent habitat.

The most favorable projection, especially in the southern two-thirds of the window, is for Gambel oak (Table 10). The projection indicates a fringe of lost habitat on the western desert edge, more persistent than threatened habitat, and large areas of emergent habitat. Douglas-fir is similar, but there is much less persistent habitat between the threatened and emergent.

Geographically, a consistent pattern is the greatest loss in the west, as desert influences expand eastward and upward. Even the Uncompahgre Plateau is unlikely to be protected from this influence. The projections show threatened habitat for Utah juniper on the shoulders of the Plateau, persistent and emergent habitat for piñon and Gambel oak, threatened Douglas-fir and a small amount of threatened aspen, with losses everywhere else. If piñon and Gambel oak can migrate, those species are likely to dominate the top and shoulders of the Plateau in the latter part of the century.

Table 10. Area of contemporary niche, its projected fate in 2060, and projected changes in niche area for 14 species in the full southwestern Colorado window.

Species	Contemporary niche (ha)	Percent Lost	Percent Threatened	Percent Persistent	Niche change 1 [a]	Niche change 2 [b]	Emergent/ Lost	Emergent/(Lost+ Threatened)
PIAR	6,879	100	0	0	-100	-100	0	0
PICO	7,482	100	0	0	-100	-100	0	0
PIFL2	4,785	99	1	0	-99	-100	0	0
PIPU	6,264	93	7	0	-93	-100	0	0
ABCO	5,623	82	18	0	-81	-99	0.01	0.01
JUSC2	12,484	51	47	2	-41	-89	0.19	0.10
POTR5	25,292	51	45	5	-31	-76	0.39	0.21
PIPO	20,008	38	51	11	-26	-77	0.32	0.14
JUOS	18,459	25	61	14	-22	-82	0.14	0.04
ABLA	16,300	36	51	14	-12	-62	0.68	0.28
PIEN	21,911	22	43	35	-7	-50	0.66	0.22
PIED	26,988	30	40	30	11	-29	1.36	0.59
PSME	20,104	14	69	16	28	-42	2.95	0.50
QUGA	22,361	5	36	58	60	23	11.87	1.56

[a] Percent change in area of the niche; considering future niche Persistent, Threatened, and Emergent.

[b] Percent change in area of the niche; considering future niche Persistent and Emergent.

Large areas of piñon are projected to be lost in the southwest. Even Gambel oak, which elsewhere may be a beneficiary of climate change, is mostly threatened with some lost in the southwest. Mesa Verde is projected to lose Gambel oak habitat in the south, and it is threatened in the north. No other species that we modeled is expected to persist in the Park, though there are areas of threatened Utah juniper.

General Management Implications

Mike Battaglia, research silviculturist with Rocky Mountain Research Station, will be developing specific vegetation management recommendations for some of the common transitions projected in the area. Here we address some general management issues and an approach to utilizing change zones.

Dealing with uncertainty

We are confident that the bioclimate models are reliable, with low error. They were developed with the best data and methods available. They reliably predict current distributions, and care was taken to include in the training data all future climates that are projected for the study area.

Less confidence can be placed in projections of future climates that are used to predict changes. While we present average model output from runs with 9 different future climate scenarios, it should be recognized that the individual climate scenarios and changes predicted from them may vary substantially. Because no climate scenario is considered more likely than another, we feel the most reasonable and practical course for managers is to consider this average.

In any case, the variations among climate scenarios can be viewed as variations in how fast the climate changes. A given climate may be predicted for 2080 by one scenario and 2050 by another, but they are all pointing in the same general direction. So the vegetation impacts that we project for 2060 may come sooner or later, but something like them is very likely.

A good way to address uncertainty in management is the use of "no-regrets" strategies, those that are beneficial under multiple scenarios and have little or no risk of socially undesired outcomes (Vose *et al.* 2012). Such actions benefit resources and values regardless of climate-change effects. Actions discussed below generally meet those criteria. If future climate change is minimal, despite all the projections to the contrary, these actions will still provide age diversity, species diversity, economic returns to communities, and facilitate recovery from disturbance. If, on the other hand, climate change is more extreme than the projections used here, we will have done the best that we currently can to provide for the conservation of genetic and habitat diversity.

Locally adapted populations and natural selection

Rather than having a single, uniform climate niche, a species is typically composed of climatypes that are genetically adapted to local climate and have varying climate niches. As the climate changes, populations may become maladapted to the new conditions (Rehfeldt *et al.* 2014b), even if the suited climatypes occur elsewhere in the window. Thus, even in persistent habitat, the local populations may not be suited to the new climate, and planting under appropriate seed transfer guidelines may be needed. Wherever we conduct planting, it is an opportunity to move seed sources upward where their climates are migrating.

Alternatively, in persistent zones, natural selection may help the local population to adapt to the changing climate. To facilitate such selection, treatments that stimulate high rates of reproduction should be encouraged. Indeed, the recent stand-replacing disturbances, such as spruce beetle, may provide the benefit of a large population of seedlings and saplings that can be selected naturally as the climate changes. However, multiple generations are needed to adapt a climatype to a new climate, and climate will be changing faster than this process can accommodate (Rehfeldt *et al.* 2014a).

Emergent habitat and migration

Emergent habitat will not be colonized quickly in many cases. Some of it is unsuitable for reasons other than climate, such as lack of soil. Otherwise it will depend on proximity to seed sources. Natural migration rates vary widely among species, but, except perhaps for a species like aspen, it is considered that natural migration is too slow to keep up with climate change (Davis *et al.* 2005).

Migration will be most successful where emergent habitat is adjacent to threatened or persistent habitat. For most species this is often the case. However, for white fir, there is no persistent habitat, and the small amount of emergent habitat is mostly isolated from current white fir. The exception is a small population of east of Trough Creek, a tributary of Saguache Creek. This is an example of a population that could be critical for conserving the species.

General use of change classes

The most important use of change zones may be not changing *how* management is done, but *where* it is done. The goal here is focusing each management action where it is likely to be most effective into the future.

LOST HABITAT – In general, do not invest in improving or managing for the future of a species here. If management is needed in such areas, favor or introduce more future-suitable replacements.

THREATENED HABITAT – Consider treating to increase resilience to drought, diseases, and insects, especially in stands where more future-suitable species can be favored.

PERSISTENT HABITAT – Normal management may proceed. If persistent habitat is limited, this may be considered a climate refugium. There may be a need to protect the species in persistent zones from stand-replacing disturbance and increase stand resilience. May be a need to import adapted populations in species whose adaptive clines are steep.

EMERGENT HABITAT – As appropriate, allow or create disturbance (fire or mechanical) to facilitate migration. Consider assisted migration as the climate changes.

A few potential examples:

- A thinning is planned in ponderosa pine to improve stand quality and growth and reduce dwarf mistletoe. There is scattered young piñon and juniper in the understory. The stand is in the PIPO Lost zone, but piñon and juniper vary between Threatened and Persistent in this area. Instead of masticating or cutting the piñon and juniper, as normally might have been done in this situation, we protect it during treatment and release it where possible, increasing the likelihood of continued tree cover through the century.

- As part of its normal timber program, a district treats about 750 acres of spruce-fir with group selection each year. Normally stands are selected within timber management areas based on stand conditions and road availability. Spruce-fir climate change zones are now added to the selection criteria. Stands in Lost zones are discriminated against, unless the stands include species that are projected to be more suited to the site in the future. Most activity takes place in Threatened and Persistent zones, increasing stand resilience, where it is most likely to be effective.

- Bristlecone pine is a valued cultural resource as well as being important to wildlife. The average projection indicates that the entire distribution in southwestern Colorado is expected to be unsuitable in 2060. Managers explore the projections of individual climate scenarios. They discover that, in several of the most favorable climate scenarios, there is a small area of Threatened habitat near Lost Mountain. The area is considered a possible climate refugium, and the decision is made to manage it to: (a) increase regeneration opportunities; (b) reduce chances of stand-destroying fire, and; (c) increase resilience to mountain pine beetle.

- An important mesa is projected to lose all habitat for species that are currently there, but piñon should have emergent habitat on the mesa top. Clark's nutcracker, Steller's jay, scrub jay, and pinyon jay are important in long-distance seed dispersal of piñon. Wildlife biologists suggest treatments to improve habitat for these birds and increase populations, especially at and above the current upper elevation of piñon. Implementing these tactics should facilitate natural migration of piñon toward the mesa top.

Acknowledgements

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Appendix: Accuracy and Uncertainty in Modeling and Projections

Bioclimate models cannot perfectly describe species distributions, because (a) there will always be a portion of the niche that is unoccupied (error of commission), and (b) there will always be favorable microsites that allow site occupancy in otherwise climatically unfavorable situations (error of omission). Likewise, projections of niche space into climates of the future are dependent on the GCMs producing the interrelationships among climate variables that exist today and, therefore, were present in the training data. Errors in vegetation data may lead to model errors. Although the best techniques were used, interpolating or downscaling climate information cannot replicate actual geographic variation in climate with complete accuracy. And finally, there will always be statistical errors in fitting mathematical algorithms to comprehensive datasets.

Climate projections are based on representative carbon pathways (i.e., emissions scenarios) that may not represent the actual future trend in greenhouse gases. This source of uncertainty can generally be viewed as uncertainty in the rate of change rather than direction. For example, conditions projected for 2060 may actually occur sooner if emissions are higher than projected, or later if they are lower. Although boundaries between change zones must be precise for planning purposes, they should be regarded as the best estimate of fuzzy boundaries, and the timing of the projected changes as likely but uncertain.

The models are quite effective at replicating the distribution of species at large scales, and are thus readily suited to regional and landscape-level planning. At smaller scales, errors can be expected, in part because climate models cannot reflect microtopographic effects or effects of recent disturbance. The best use of projections at small scales will be in conjunction with the expertise of managers well acquainted with the area.

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