

Adapting forest management to climate change using bioclimate models with topographic drivers

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Bioclimate models incorporating topographic predictors as surrogates for microclimate effects are developed for *Populus tremuloides* and *Picea engelmannii* to provide the fine-grained specificity to local terrain required for adapting management of three Colorado (USA) national forests (1.28 million ha) and their periphery to climate change. Models were built with the Random Forests classification tree using presence–absence observations obtained by overlaying species distribution maps on data points gridded at ~225 m within the forests and from ground plot observations from adjacent areas. Topographic effects derived from 90-m elevation grids were expressed by weighting aspect by slope angle. Climate estimates were obtained from spline surfaces. Out-of-bag errors were ~17 per cent, and classification errors for an independent sample from within the forest were ~13 per cent. Topographic variables were second in importance to climate variables for predicting species distributions; their inclusion captured well-known topographic effects on vegetation in mountainous terrain. Predictions made for future climates described by three General Circulation Models and three emissions scenarios were used to map on 90-m grids the habitat expected to be lost, threatened, persistent or emergent. The habitat categories are used to identify those areas where treatments should have highest likelihood of success.

Introduction

Rates of climate change are projected to be much faster than natural systems can respond such that a quasi-equilibrium is maintained between plant distributions and climate (e.g. Rehfeldt *et al.*, 1996; Solomon and Kirilenko, 1997; Davis *et al.*, 2005). Adjustment to change, therefore, will be governed by the time lags imbedded in ecological processes: lags between cause and effect occurring at the trailing edge as the changing climate exceeds the physiologic plasticity of individuals (e.g. Mátyás *et al.*, 2010); migration lags on the leading edge developing from the contingencies of seed dispersal and colonization (Davis, 1989; Davis and Shaw, 2001); and adaptation lags (Mátyás, 1990; Davis *et al.*, 2005) arising between the edges as microevolution restores fitness of species becoming less well attuned physiologically to the climate they inhabit. Considered together, these effects portend widespread disruption to the vegetation, a conclusion inferred unanimously by numerous researchers (e.g. Rehfeldt *et al.*, 2006). Dependence on natural processes, therefore, seems destined for negative long-term effects on the amenities and services that humans expect from native ecosystems, particularly those dominated by long-lived, sessile forest trees (see Joyce and Rehfeldt, 2013; Rehfeldt *et al.*, 2014c).

Proactive strategies, designed for anticipating and responding to the impacts of climate change, promote the deliberate intervention in natural process with the goal of increasing the capacity of

ecosystems to survive and function at levels acceptable to humans (Scholes *et al.*, 2014). Such strategies are focused primarily on reducing ecosystem vulnerability and enhancing recovery (Spittlehouse and Stewart, 2004). While demands for action are being made on forest managers (Peterson *et al.*, 2011), the necessary tools and guidelines are emerging slowly (Innes *et al.*, 2009). Abundant literature describes and debates conceptual approaches, strategic frameworks, procedures for analysing goals and information networks to support the planning process, but few concrete examples exist for developing and deploying actual, practical plans (but see Crookston *et al.*, 2010; Klenk and Larson, 2015), particularly at the landscape scale.

We envision an approach similar to Janowiak *et al.* (2014) that begins with a thorough assessment of climate-change impacts. Once potential impacts are understood, managers can focus limited resources where they can be the most effective, that is, implement resilience and recovery tactics where threats are greatest, assist migration where new habitat is emerging or conduct traditional management where species should persist. By defining ecologic optima climatically and designing plans to exploit these optima, this approach relies less on risk assessment and more on identifying where projected impacts are most likely to occur.

Our primary objective is to develop species-specific bioclimate models driven by climate and topographic variables to predict the occurrence of suitable habitat from presence–absence

data. Topographic variables are envisioned as surrogates for micro-climate effects derived from interactions of aspect and slope angle that are well known but difficult to quantify. While bioclimate models have a demonstrated utility for assessing impacts of a changing climate on plant distributions, the finest resolution at which such models have been applied heretofore has been on 0.008333° grids, that is, 1 km when measured at the equator. For much of the forested lands in the North America's mountainous west, however, considerable physiographic, climatic and vegetal diversity can occur within 1-km grid cells. By incorporating topographic effects into modelled distributions, we develop applications at 90-m resolution, which, therefore, are of greater potential utility.

Our secondary objective is to provide a management strategy for accommodating climate change. We use for illustration the Grand Mesa, Uncompahgre and Gunnison National Forests (GMUG) of western Colorado (Figure 1), taking advantage of the fine-scale vegetation maps developed by the forests. We consider their two most prominent tree species, *Populus tremuloides* (trembling aspen, hereafter, aspen) and *Picea engelmannii* (Engelmann spruce, hereafter, spruce), and use the reference period 1961–1990 to represent the longer period of climate associated with current distributions. Climate normals for this 30-year period, moreover, are considered to be the baseline from which impacts of global warming are measured. Projections target climates in the decade surrounding 2060, as described by General Circulation

Models (GCMs). The decade of 2060 is sufficiently distant such that management decisions will have time to develop or to be revised, but not so far in the future that trends are uncertain. We view the well-documented temporal uncertainties in GCM projections as less relevant than the high likelihood that a given impact will occur, encouraging land managers to focus on climate-change trajectories rather than on precise timing.

Setting and background

The physiographic diversity, pending management issues and fine-scale vegetation maps make the GMUG an ideal location for developing proactive strategies from vegetation models. The GMUG straddles two physiographic provinces, the Southern Rocky Mountains and the Colorado Plateau, in southwestern Colorado, USA. The eastern and southeastern boundaries are formed by the Continental Divide (Figure 1). These national forests encompass 1.28 million ha but are dispersed within an area of ~ 3.7 million ha, giving for our work the geographic window of 37.5° to 39.5° latitude and -109° to -106° longitude (Figure 1). Elevations within this window range from ~ 1700 to 4400 m.

Vegetation on the GMUG ranges from semi-desert to alpine, with the intervening vegetation varying considerably depending on topography, substrate and disturbance history. Aspen and spruce-fir cover types, the latter composed of spruce with usually a lesser amount of *Abies lasiocarpa*, each occupy ~ 36 per cent of

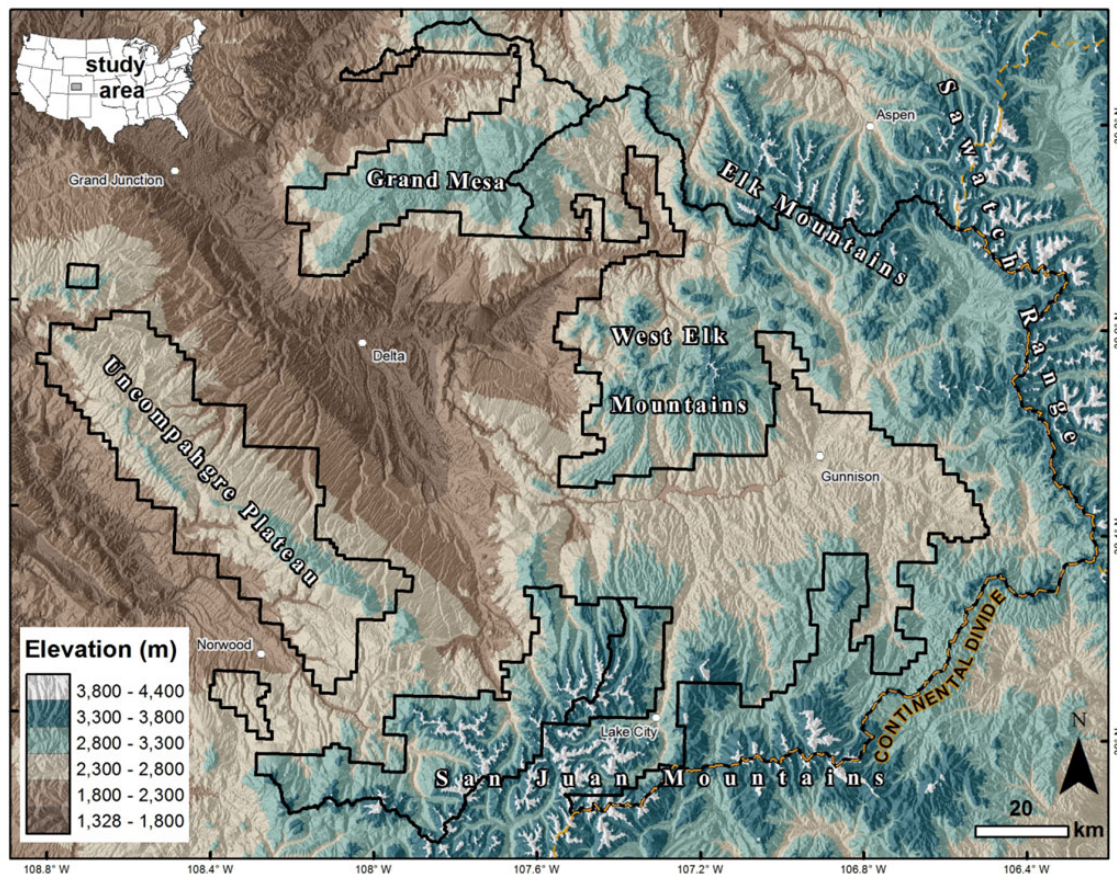


Figure 1 Physiography of the region of study locating the Grand Mesa, Uncompahgre and Gunnison National Forests (black outlines).

the forested area or 22 per cent of the GMUG [see http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev7_003170.pdf (accessed on 28 March 2014)]. Both cover types are valued for scenery, wildlife habitat, watershed protection and wood products. Whereas the scenic beauty of aspen is a major contributor to the tourism economy, spruce is the most valuable timber species. Other notable cover types include Gambel oak (*Quercus gambelii*) at 9 per cent of the forest, lodgepole pine (*Pinus contorta*) at 8 per cent and bare rock at 7 per cent.

Two major climate-related disturbances are occurring within the aspen and spruce-fir cover types in the GMUG. A spruce beetle epidemic that had been building in the region exploded in 2010, infesting ~10 000 ha by 2014 (Brian Howell, USDA Forest Service, personal communication). A warming climate affects beetle epidemics primarily by increasing host moisture stress, thereby compromising defence responses (Hebertson and Jenkins, 2008). Aspen has been severely impacted by a turn-of-the-century drought, which incited sudden aspen decline (SAD) on 96 000 ha, comprising 33 per cent of the aspen cover type (Worrall *et al.*, 2008, 2010). Although spread of the decline ceased by 2010, affected stands have continued to deteriorate (J.J. Worrall, unpublished results). The GMUG is currently engaged in developing management responses to these disturbances.

Methods

Our analyses rely on species distribution maps that we assembled from FSveg [Field Sampled Vegetation, see <http://www.fs.fed.us/nrm/fsveg/> (accessed on 3 March 2014)], a data storage system describing vegetation inventories as inferred primarily from aerial photography but also updated periodically from ground observations. FSveg data are generally unavailable outside the national forest boundaries. In the vernacular of FSveg, our distribution maps included all polygons for which aspen or spruce were listed as one of the three most prominent species in the Dominant Life Form or Majority Life Form vegetation descriptors. Our maps, therefore, are actual distributions minus isolated occurrences of individual trees in mixed stands. These maps, moreover, are of extremely high resolution. The spruce distribution map, for instance, has 26 186 polygons that are as small as 0.05 ha and as large as 1333 ha; 89 per cent are <40 ha, and 51 per cent are <10 ha.

The database from which bioclimate models were developed was obtained by exporting 250 000 locations regularly spaced within the boundary of the GMUG (Figure 1), using the *sp* package (Pebesma and Bivand, 2005; Bivand *et al.*, 2013) in R (R Core Team, 2014). This sampling density approximated a 225-m grid, that is, one data point representing ~5 ha. The presence or absence of each species was determined at each sample point by using R's *mapttools* package (Bivand and Lewin-Koh, 2014) on FSveg. *Maptools* was also used to identify polygons not included in the samples, ~5000 for each species. A single data point was obtained at a random location from within each of these polygons, and their locations were appended to the appropriate presence-absence data set. Presence-absence observations beyond the forest boundary but within the window of Figure 1 were obtained for 680 ground plots from FIA [Forest Inventory and Analysis, <http://www.fia.fs.fed.us/tools-data/> (accessed on 21 June 2012)]. The density of these plots was smaller by far than data points within the GMUG and is included so that the area peripheral to the forest was not subject entirely to extrapolation.

Elevation (m) was assigned to each observation from the 90-m grids of SRTM (Shuttle Radar Topographic Mission, Jarvis *et al.*, 2008), and aspect (degrees azimuth) and slope angle (°) were estimated with the GRASS package (GRASS Development Team, 2012) in R. Climate estimates for the reference period (1961–1990) were obtained from thin plate spline surfaces [<http://forest.moscowfsl.wsu.edu/climate/> (accessed on 4 March

2014)], which, being continuous, are not dependent on grids and their resolutions. Monthly temperature and precipitation were used to construct climate variables (Rehfeldt *et al.*, 2006) either derived directly from monthly means or involving interactions among the derived variables.

Two topographic vectors were constructed from the product of slope angle (radians $\times 10^{-2}$) with either the sine or cosine of aspect (° azimuth converted to radians) (Stage, 1976), thus producing east-west and north-south vectors, respectively, weighted by slope steepness. We refer to these two weighted vectors subsequently as topographic vectors.

The Random Forests classification tree of Breiman (2001) in R was used to develop separate bioclimate models for aspen and spruce (see Rehfeldt *et al.*, 2006; Worrall *et al.*, 2013). Because the presence of aspen and spruce in their respective data sets was ~39 per cent, subsampling was not necessary to satisfy Breiman's condition for reasonable balance in the number of observations per class. Therefore, the models were developed from ~255 000 observations using 200 'trees' in one 'forest'. In this algorithm, each 'tree' produces an independent estimate of model parameters based on a unique subsample of the observations. In making a prediction, new observations are exposed in each 'tree' to a hierarchy of decisions that result in a classification. Each 'tree' casts one vote, which, in our case, is whether or not the climate associated with an observation is suitable for the species. The voting threshold used for judging suitability frequently is set at 50 per cent, the majority. Thresholds, however, can be set to best suit the goals of the analysis. The 40 per cent threshold, for instance, might be used when errors of omission are of greater concern than errors of commission.

A stepwise elimination procedure was used to choose the predictor variables to be included in the bioclimate model. The stepwise process began with 31 climate predictors and 2 topographic predictors and ended with 1 variable remaining. The mean decrease in accuracy was used at each step to judge variable importance, and the most important predictor was considered to be the last variable remaining. Out-of-bag errors were used to select a reasonably parsimonious combination of variables to be included in the bioclimate model. These errors are calculated from observations withheld internally by the Random Forest algorithm during the construction of each tree.

To map predictions from the models, we produced 90-m grids for the array of climate variables by running SRTM grids across the spline climate surfaces. These grids plus the topographic grids were run through the bioclimate models to obtain votes of climate suitability for each cell of the SRTM grid.

Model verification for the GMUG portion of our geographic window was approached in two ways, both of which used data independent of those used to build the models. Both assumed that the distribution maps were without error. One compared presence predicted for all cells on the 90-m grid (using a 50 per cent voting threshold to predict presence) with presence-absence on the distribution maps. However, because physiographic diversity is often present within grid cells, a point estimate receiving >50 per cent of the votes could reside within a grid cell receiving <50 per cent. For the second comparison, therefore, a new sample of one million GMUG point locations was run across the species distribution maps and through the bioclimate models so that predictions, based on the 50 per cent voting threshold, could be compared with observed distributions.

To assess potential impacts of climate change, projections were made for the decade 2055–2064 using output from three GCMs and three scenarios for greenhouse gas emissions (RCP4.5, RCP6.0 and RCP8.5; the RCP2.6 scenario is ignored because assumptions of reduced emissions already are invalid). GCM output was obtained from CMIP AR5 [<http://cmip-pcmdi.llnl.gov/cmip5/> (accessed on 11 August 2014)] for CCSM4 from the Community Earth System [<http://www.cesm.ucar.edu/models/ccsm4.0/> (accessed on 11 August 2014)], GFDLCM3 from the Geophysical Fluid Dynamics Laboratory [<http://www.gfdl.noaa.gov/coupled-physical-model-cm3> (accessed on 11 August 2014)] and HadGEM2ES from the Met Office, UK [<http://www.metoffice.gov.uk/research/modelling-systems/unified-model/climate-models/hadgem2> (accessed on 11 August 2014)]. For mapping, the climate grids at <http://forest.moscowfsl.wsu.edu/climate/> (accessed on 4 March 2014) were

recalibrated for the 90-m grids of SRTM using the window of (Figure 1). Maps were made for the mean votes of nine projections (3 GCMs × 3 scenarios) to produce a single grid from which practical inferences could be drawn.

Results

We chose 8-variable models as being reasonably parsimonious while providing a measure of assurance that projections would not be dependent on single variables (Rehfeldt et al., 2006). Out-of-bag errors were ~16 and 17 per cent for the aspen and spruce models, respectively (Table 1). Of them, errors of commission were slightly higher than errors of omission.

The most important predictor of aspen’s distribution was the mean maximum temperature in the warmest month, followed sequentially by the summer – winter temperature differential and the topographic vectors. Of the latter two, the east-west vector was of slightly greater importance than the north-south vector. The other variables were the length of the frost-free period, a winter temperature sum based on the monthly minimum, winter temperatures weighted by an annual dryness index and an interaction of annual precipitation with growing season degree-days. For spruce, greatest importance was shared by the length of frost-free period and the east-west topographic vector. Third in importance were winter temperatures weighted by an annual dryness index followed by the summer–winter temperature differential, the north-south topographic vector, two variables describing winter cold and winter precipitation.

In the two verification exercises, errors of prediction using a sample of data points independent of those used to build the models produced essentially the same error estimates as those based on pixel counts for the 90-m grid, that is, ~13 per cent for the aspen model and ~14 per cent for the spruce model (Table 1). Both estimates were ~3 points lower than the out-of-bag errors. These exercises also showed errors of omission to be somewhat higher than errors of commission, a trend inconsistent with the out-of-bag errors.

Mapped predictions (Figure 2) convincingly illustrate the accuracy of the models in representing the distribution of species for the

reference period, despite errors of fit that may seem large intuitively. The inserts in Figure 2 were selected to illustrate the most flagrant examples of commission and omission errors, the categories labelled ‘incorrect absence’ and ‘incorrect presence’, respectively. The figure shows errors of omission, for instance, to be common within (a) linear polygons which are mostly dispersed in favourable microsites along valley floors (insert A, both maps) or (b) along the edges of larger polygons where either the models or distribution maps failed to precisely locate changes in the vegetation (insert B, both maps). Yet, correct predictions were made for individual grid cells even for those polygons otherwise poorly represented by the models (insert C, both maps). Errors of commission, moreover, sometimes occurred at the edges of polygons but mostly were scattered within large polygons.

Effects of including the topographic vectors to modify climate predictors are evident in the panels of Figure 3. Bioclimate models driven solely by climate variables tend to predict constant effects along a contour because effects of aspect and slope angle ordinarily are not considered. Yet, as shown in Figure 3, predicted distributions of aspen and spruce along the contours surrounding the mountain peaks are closely related to topography. Southern and southwestern aspects, for instance, tend to have more aspen and less spruce than northern aspects.

Potential impacts of climate change are readily illustrated (Figure 4) from the change in votes between the reference period and the decade of 2060. In calculating this difference, the proportion of votes for the reference period was subtracted from the average of nine future projections, resulting in a value of +1 when the votes were zero for the reference period but 100 per cent for the future, or –1 when 100 per cent for the reference period but zero for the future. In the figure, therefore, dark purple represents lost habitat whereas dark green represents emergent habitat. The figure illustrates that by mid-century, unsuitable climate could be widespread in the current aspen and spruce forests (Figure 4), a conclusion consistent with previous work with these species (Rehfeldt et al., 2006, 2009; Worrall et al., 2013).

To provide land managers with tools suitable for decision-making, we applied the logic of Table 2 to the change in votes (Figure 4) to classify aspen and spruce habitat into lost, threatened, persistent and emergent categories (Figure 5). Basic to our classification is the degree of confidence generated from model output. Voting proportions of >0.7 convey high confidence in suitability whereas proportions of <0.3 convey high confidence in unsuitability. For lands to be classified as lost habitat, confidence should be high that species will perish. Habitats for which the votes are equivocal are classified as threatened, that is, low confidence in the habitat being either lost or persistent.

Interpreting the votes in this way allows habitat to be apportioned according to expectations for the future (Table 2). About 52 per cent of the current aspen distribution and 22 per cent of the current spruce distribution is classified as ‘lost’, that is, no longer being suitable for these species by mid-century or beyond. Large portions, 42 per cent for aspen and 58 per cent for spruce, appear in the threatened category, and as a result, a scant 7 per cent of contemporary aspen habitat and 19 per cent of the contemporary spruce habitat would remain suitable for these species through mid-century. While an optimist would conclude that these statistics portend demise of about one-half of the contemporary aspen and one-quarter of the contemporary spruce distributions, a pessimist would conclude that the loss could be as much as 94 per cent for

Table 1 Errors of prediction summarized by three techniques: classification errors produced by the random forests models, model verification with independent data for the GMUG and mapped pixel counts of observed and predicted

Source of error	Random Forest algorithm ¹	GMUG verification ²	GMUG pixel count ²
Aspen			
Overall	16.1	13.2	13.3
Omission	14.5	14.5	14.5
Commission	18.5	12.4	12.5
Spruce			
Overall	17.1	14.1	14.1
Omission	16.2	14.6	14.5
Commission	18.5	13.8	13.8

Note: errors of omission are the percentage of presence observations misclassified; errors of commission are the percentage of absence observations misclassified.

¹Out-of-bag error.

²Based on voting threshold of 50 per cent.

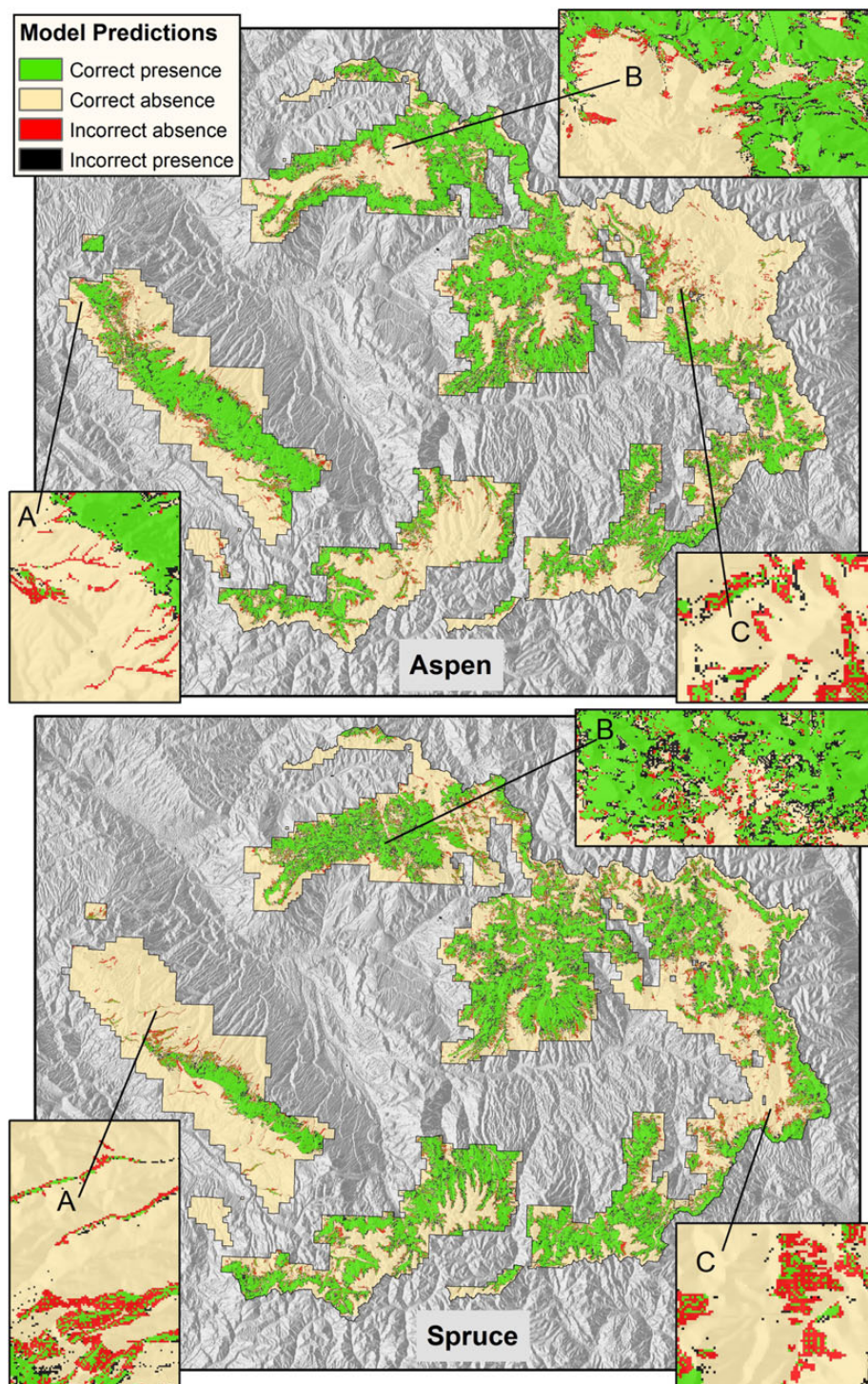


Figure 2 Predictions of presence or absence (50 % voting threshold) and their errors from a Random Forests classification tree for the Grand Mesa, Uncompahgre and Gunnison National Forests mapped at 90-m resolution.

aspen and 80 per cent for spruce, with outcome being determined by the fate of trees within the threatened category.

New habitat in the emergent category would offset the losses to some extent, but future distributions nonetheless should be

smaller. The amount of reduction, however, again is dependent on the fate of trees in the threatened category and falls, therefore, within a broad range: by 11–53 per cent for aspen and 6–64 per cent for spruce.

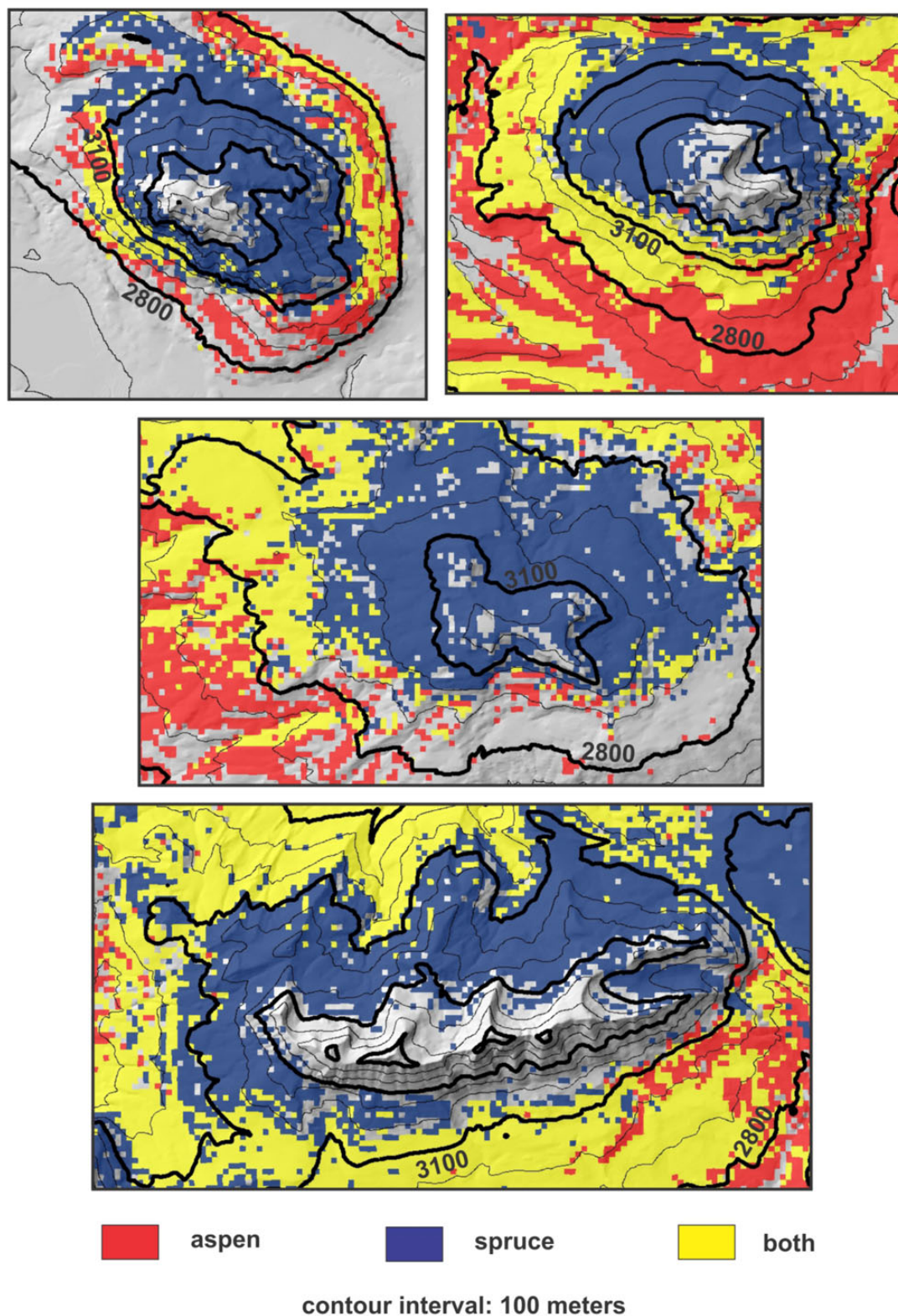


Figure 3 Four panels within West Elk Mountains (Figure 1) illustrating influence of topographic drivers on predicting suitable habitat from a Random Forests classification trees using the 50 per cent voting threshold and mapping at 90-m resolution.

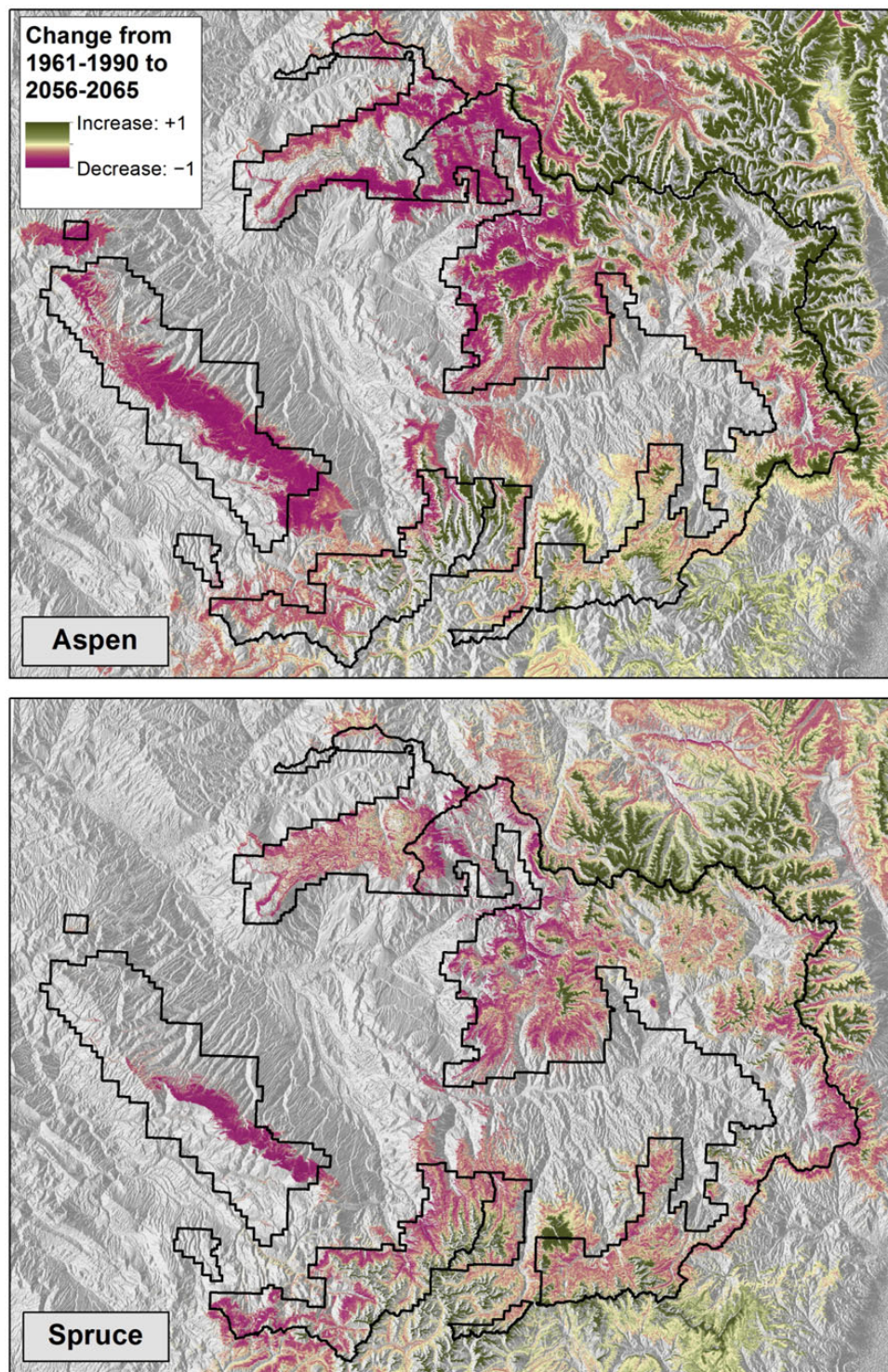


Figure 4 Difference in votes between future projections and contemporary predictions as generated by a Random Forests classification tree mapped at 90-m resolution. Votes for the future period are averages produced from projections using three GCMs and three emissions scenarios.

Discussion

By using the combined effects of aspect and slope angle in association with climate predictors, our approach incorporates surrogates for microclimate effects known to impact the local distribution

of plants. The topographic vectors we used aptly describe these effects, became important components of the statistical models and provided realistic topographic modifications of climate suited to predicting the occurrence of two species. Because the topographic vectors are available at fine scales, the distribution of aspen and

Table 2 Logic for classifying habitat from votes generated by the bioclimate models and the resulting areal statistics for aspen and spruce habitat for the geographic window of Figure 1

Habitat classes	Voting logic (proportions)		Aspen area		Spruce area	
	Reference period	Mid-century ¹	Hectares (thousands)	Per cent ²	Hectares (thousands)	Per cent ²
Lost	≥0.5	<0.3	799	52	356	22
Threatened	≥0.5	≥0.3 and <0.5	641	42	936	58
Persistent	≥0.5	≥0.5	140	7	310	19
Emergent	<0.5	≥0.5	636	41	268	16

¹Calculated from the mean of nine projections (3 GCMs × 3 carbon scenarios) for 2054–2065.

²Based on area occupied in the reference period.

spruce habitats described by the models can be mapped at resolutions amenable to forest management.

Our models captured the essence of the aspen and spruce habitat distributions on the GMUG, despite errors of fit that were nearly twice those reported previously for the same species (Rehfeldt *et al.*, 2006, 2009; Worrall *et al.*, 2013). Some of this error, however, is not necessarily related to the modelling procedures. Errors of prediction that are concentrated at the periphery of large polygons tend to be associated with ecotones that undoubtedly presented difficulties to those mapping cover types. Linear distributions, another source of prediction errors, may be missed easily in a systematic sample. Errors of commission occurring within large polygons, moreover, can be related to microsites not suited to forests because, for instance, of unsuitable substrates, such as the rock outcrops that cover ~7 per cent of the GMUG. An additional factor leading to the absence of species when the climate is suitable is a disturbance history that may preclude occurrence even when the climate is ideal.

Although measures such as increasing sampling intensity or eliminating polygons of lakes, reservoirs or bare rock could be taken in an attempt to reduce modelling errors, the distribution of errors in Figure 2 suggests that the exercise would be of limited practical value. With an ability to represent the contemporary distribution of suitable habitat for aspen and spruce, the models display an accuracy that makes them useful tools for managers.

Projections from our models (Figure 4) parallel closely results from previous studies of both aspen (Rehfeldt *et al.*, 2009; Worrall *et al.*, 2013) and spruce (Rehfeldt *et al.*, 2006): the climate inhabited by these species today is destined to move upwards as the climate continues to change. Loss of habitat at the trailing edge would be insufficiently counterbalanced by gains at the leading edge to result in a net loss of habitat. This upward shift of suitable habitat has additional ramifications for adaptation of forest trees. In broad ranging species like aspen and spruce, genetic variability for adaptive traits has been moulded by evolutionary processes into clines that tend to parallel temperature gradients (see Morgenstern, 1996). For regions such as the GMUG where altitudinal gradients are long and steep, one can anticipate genetic differences among populations for adaptive traits to be arranged along clines that parallel the climate gradients. As the climate changes, populations become less well suited genetically to the environment that they inhabit (for discussion, see Rehfeldt *et al.*, 2014c). This means that our category of persistent habitat does not necessarily imply that the genotypes currently inhabiting these areas will continue to be optimal genetically in future climates. To be sure, this upward

shift of suitable habitat portends widespread disruption of GMUG ecosystems.

In considering genetic responses to climate, the aspen and spruce forests of the GMUG would represent only a portion of a range-wide cline. It is likely, therefore, that populations of these species exist elsewhere that are preadapted to future climates of the GMUG. To assess this possibility, we used bioclimate models for western USA (Rehfeldt *et al.*, 2006, 2009), even though they included no topographic drivers, to screen the FIA database for contemporary locations suited to future climates in the GMUG’s lost and threatened categories. The exercise suggested that ~8 per cent of aspen’s lost category and 50 per cent of the threatened category could be upgraded to the persistent category if they were to be inhabited by genotypes from populations currently occurring in three clusters: one 250 km to the north and two 300 or 500 km to the west. However, the exercise also identified FIA locations from the GMUG itself as being suited to future climates in the lost category, thereby underscoring the futility of such imputation analyses unless either (1) additional models using topographic drivers were available for peripheral regions or (2) the microclimate effects of aspect and slope could be quantified. Until then, natural systems must rely on evolutionary processes in genetically diverse reproduction to produce and maintain adaptive clines in future climate space. This exercise nonetheless demonstrates that projections particularly for the threatened category of Figure 5 may not be quite as dire as implied.

To be sure, high uncertainty surrounds projections for future climates. The size of the threatened category in Table 2 expresses this uncertainty, the effect of which is a broad range of possible habitat losses for these two species by mid-century or soon thereafter: 11–53 per cent for aspen and 6–64 per cent for spruce. Also uncertain is the speed at which the effects will accrue (see for example Rehfeldt *et al.*, 2014b). Yet, climate-induced events currently affecting GMUG aspen and spruce are engaging land managers, despite uncertainties about the future. Our approach is to provide managers with guidelines based on the best information available today while acknowledging that as more information and experience accrues, guidelines need to change.

Adapting management to climate change

Of the topics needing integration into traditional forest management to accommodate climate change, we concentrate on aiding recovery from damage, increasing resilience and facilitating

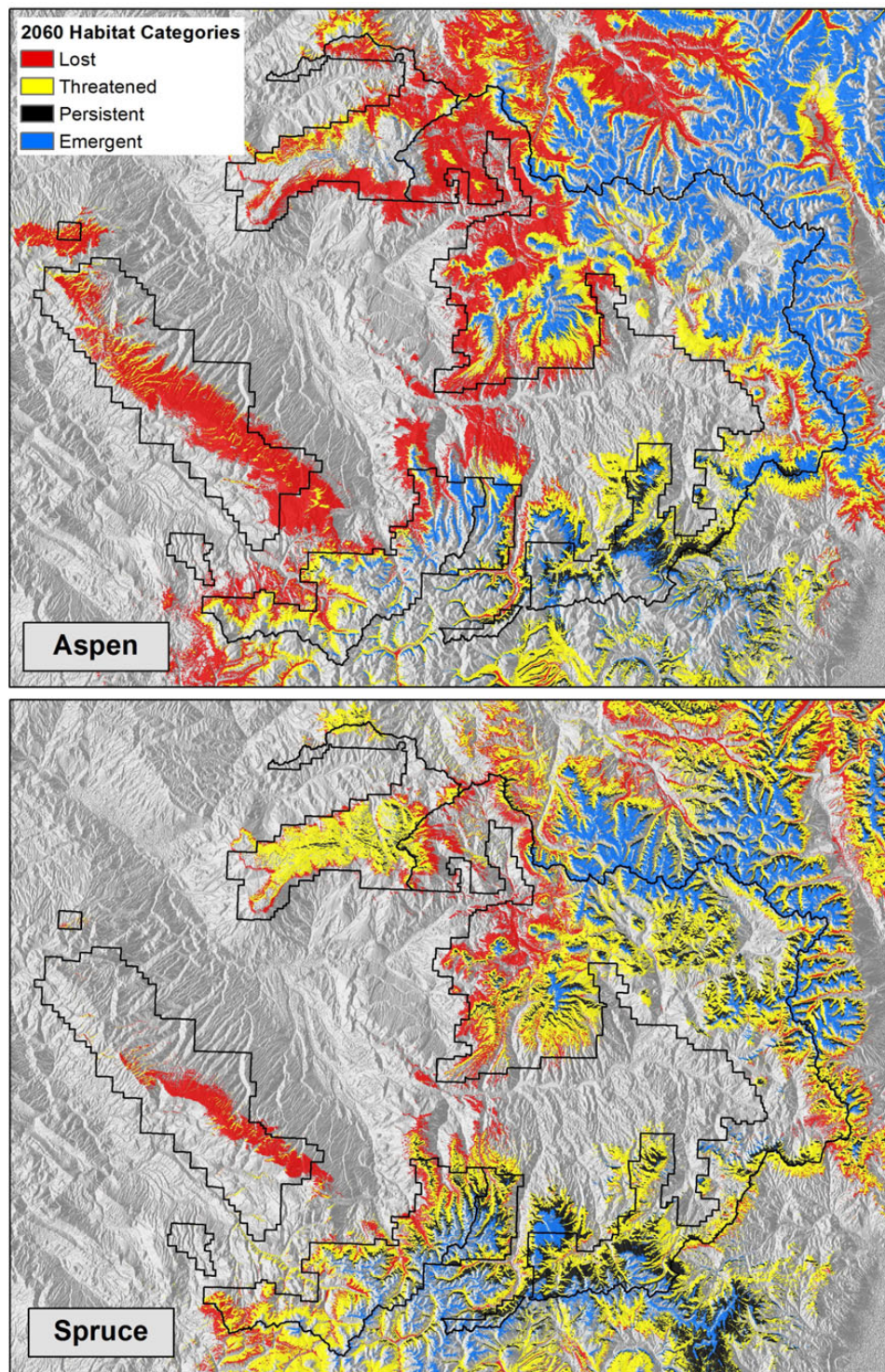


Figure 5 Habitat classifications based on the categories defined in Table 2 and mapped at 90-m resolution.

or assisting migration. By using the habitat classes of Table 2 and Figure 4, we outline management guidelines that would channel resources to where they are most likely to be effective (see also Janowiak *et al.*, 2014).

Aspen

Aspen's GMUG distribution is dominated by age classes of >40 years, the ages most susceptible to SAD (Worrall *et al.*, 2013). Resiliency, therefore, is a primary consideration in aspen management,

achievable by diversifying age classes across forested landscapes by using natural disturbances, prescribed fire or mechanical prescriptions to promote clonal reproduction. Stand treatments where herbivore pressures are high, however, must also consider steps to alleviate browsing impacts, either by fencing or by treating tracts large enough to absorb the pressures. Such treatments seem best suited to lands in the threatened category, but would be suitable for all aspen sufficiently healthy to regenerate. Lands containing beetle-killed spruce with scattered aspen also would qualify.

Recovery of aspen stands afflicted with SAD is possible if regeneration occurs before basal area losses are >50 per cent, provided that the remaining overstory is healthy (Ohms, 2003; Shepperd *et al.*, 2015). Overstory removal to stimulate suckering, either mechanically or by fire, would be particularly suited for lands in the threatened and persistent categories.

Encouraging aspen migration has the potential of addressing dual goals, as ~43 per cent of the land in aspen's emergent category is spruce habitats classified as lost or threatened. As spruce succumbs to spruce beetle, fire or drought in these habitats, an appropriate management action would be to facilitate aspen migration (Landhäusser *et al.*, 2012). However, procedures appropriate for securing either natural or artificial regeneration are not yet established. Although the efficacy of reproduction via seeds in Rocky Mountain aspen forests has long been questioned, fecund females (Long and Mock, 2012) tend to produce lightweight, wind-dispersed seeds with high germination rates. Seedlings, moreover, have been found up to 18 km from mature trees (Turner *et al.*, 2003). With sexual reproduction more widespread than formerly thought (Mock *et al.*, 2008) and suckering after seedling establishment not at issue (Fairweather *et al.*, 2014), stimulating migration via natural reproduction would seem to be a viable option. Yet, a dioecious sexuality, the occurrence of triploid cytotypes at high frequencies in the Rocky Mountains (Mock *et al.*, 2012) and seedbed requirements for exposed mineral soil can interfere with obtaining reasonably well-stocked regeneration (Karen Mock, personal communications, and Johanna Nosal, personal communications). Consequently, artificial regeneration may be necessary for assuring timely migration. Although aspen nursery and planting techniques have been studied (e.g. Landhäusser *et al.*, 2012), operational planting programmes are not well developed in the GMUG region (Wayne Shepperd, personal communication). Investment in nursery operations and practices, therefore, would be required for planting to become a viable option.

Although aspen may persist on favourable microsites within habitat projected to be lost, active management to either favour or perpetuate aspen seems futile unless objectives are short-term; treatments are much more likely to be effective within the persistent, threatened or emergent categories. Migration upwards of woodland, shrub or grassland communities into lands in the lost category is both expected (Rehfeldt *et al.*, 2012) and apparently underway (Anderegg *et al.*, 2012), but additional analyses specifically targeting GMUG vegetation are needed for managing additional cover-type conversions.

Spruce

In spruce habitat classified as threatened or persistent, enhancing resilience to both drought and the spruce beetle is urgently needed. Resilience of established stands can be augmented by reductions in basal area, thereby alleviating drought stress to residual trees

(Innes *et al.*, 2009; Peterson *et al.*, 2011). Basal area reductions can be accomplished by increasing group size in group-selection management systems or using shelterwood systems, both of which, however, are limited to landscapes where thinning operations are feasible. Decreasing the proportion of spruce in mixed stands also can reduce the risk and severity of beetle impacts (Schmid and Frye, 1976). Investing in treatments for habitat expected to be lost seems unwarranted unless either long-term objectives are for species conversions or short-term objectives such as conservation or recreation are overriding.

Replacing beetle-killed spruce forests with planted spruce seems particularly suited for persistent habitat but also should be appropriate on high-quality sites within the threatened category. Maintaining forest health and productivity by means of artificial regeneration, however, requires planting trees in the climates for which they are genetically suited (Rehfeldt, 2004). Because the climate to which contemporary populations are adapted is warming, maintaining health of planted trees requires moving contemporary sources of seeds upwards into climates projected to be suitable in the near future, that is, assisting their migration (Innes *et al.*, 2009). New seed transfer guidelines are needed that will maximize the genetic flexibility of transferred populations for coping with uncertainties of the future.

Much of the spruce habitat classified as emergent currently is inhabited by alpine vegetation. These lands, however, should continue to be unsuitable for spruce because factors other than climate (e.g. unstable slopes and absence of soil) are limiting. Where site conditions are suitable, natural reproduction should gradually become established (Daly and Shankman, 1985) and, therefore, where soils exist, planting programmes also can be considered. However, until seed transfer protocols are established, migration should be limited to ~100 m or so in elevation, within which natural dispersal is common.

Spruce habitat projected to be lost should gradually become suited for vegetation better suited to warm and dry conditions, even though the sporadic occurrence of moist microsites may allow spruce to persist as isolated outliers. Visualizing the vegetation destined to replace spruce, however, is not necessarily straightforward. While aspen will be suited to a portion, some also should become suited for species such as *Juniperus* spp., *Pinus contorta*, *Picea pungens* and *Pseudotsuga menziesii*, although the outlook for the latter species is not necessarily promising (e.g. Rehfeldt *et al.*, 2014a). These considerations, like those for aspen, point to the need for comprehensive studies that consider vegetation in addition to aspen and spruce.

Other considerations

Contemporary decline of aspen forests is combined with spruce beetle outbreaks to produce conditions on the GMUG requiring the immediate attention of land managers. Because these events are coupled with large projected impacts from the changing climate, conditions on the GMUG are opportune for adapting forest management to climate change. Widespread mortality is occurring and is expected to continue in forest types likely to become unsuitable for future climates. Extensive landscapes, therefore, will be available for programmes designed to renew forests such that health, growth and productivity are maintained (Rehfeldt *et al.*, 2014b). Yet, the GMUG contains extensive lands designated

as wilderness or roadless within which adjustment to change will proceed naturally.

Our proposals for adapting management to climate change are 'no-regrets' strategies (Vose *et al.*, 2012). Such strategies incorporate programmes designed for low risk in the event of an undesirable outcome despite the uncertainties surrounding the future. Beneficial outcomes, therefore, are expected from such programmes regardless of the uncertainties. Our strategy for the GMUG is comprised of such actions. If, on the one hand, rates of climate change are less than projected by most GCMs, the actions we advocate nonetheless will provide for the perpetuation of forests with enhanced resiliency. If, on the other hand, rates of change are more extreme than projected, the actions we propose would foster forest health, but for shorter time intervals than planned.

Microsites suitable for the perpetuation of aspen and spruce undoubtedly will either persist or arise within our 'lost habitat' categories. Our results and their applications neither preclude the occurrence of such stands nor imply that they would not benefit from management. In accord with the 'no-regrets' strategy, however, scarce resources are invested where possibilities of success are highest. In our view, these areas will be those for which the models convey the highest confidence that the future climate will be suitable, that is, within categories other than lost.

In planning courses of action using modelled responses projected into future climates, accuracy of the models and uncertainty about the future are concerns frequently voiced. In regard to the first of these, we show in Figure 2 that the errors of prediction tended to be associated with polygon borders, thereby having little effect on describing the general distribution of the polygons themselves. The topographic vectors, moreover, account for well-known effects of aspect and slope angle on species distributions to convey accuracies in predicting suitable habitat not ordinarily available from vegetation models. The uncertainties surrounding GCM output are not only well documented but also are frequently used as an excuse to stymie proaction. Yet, whether any one GCM or scenario will turn out to have been accurate is not the question that should control decision-making. The many GCMs and scenarios describe similar impacts to the vegetation that vary primarily in timing. By (a) recognizing that GCM output for the decade surrounding 2060 translates into impacts expected sometime for mid-century or beyond and (b) focusing on agreement among projections rather than their variation, managers can evade the inertia bred by uncertainty.

Our models predict and project the climatic limits of the realized niche, the portion of the fundamental niche where the biotic and abiotic environments allow a species to persist. The specificity of projections depends, therefore, on a static realized niche. While factors such as succession, substrate, fire frequency, insect and disease outbreaks, or grazing may affect the proportion of the niche that is occupied, they do not necessarily impact the climatic limits of the niche itself. Factors capable of altering niche limits include evolutionary responses in insects and diseases, but concern tends to be centred about possibilities of future climates having no contemporary analogues (e.g. Williams *et al.*, 2007) where, presumably, competitive regimes would change (Jackson *et al.*, 2009), thereby changing also the climatic limits of the realized niche. Although GCM output can be used to demonstrate that future climates of the GMUG should have historical precedence (see Rehfeldt *et al.*, 2012), the potential influence of enhanced climate variability on analogues has not been

investigated. For this reason alone, practical programmes need a solid foundation in 'no regrets' strategies.

In developing programmes for a changing climate whose timing is uncertain but whose direction is known, one course of action is obviously fallacious: implementing the well-established programmes designed for the static climates of yesterday doubtlessly will lead to negative outcomes. We advocate assembling the best information available today, designing programmes to minimize risk and relying on land managers of the future to adjust programmes as impacts accrue.

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Conflict of interest statement

None declared.

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