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ORIGINAL ARTICLE

# Influence of bioclimatic variables on tree-line conifer distribution in the Greater Yellowstone Ecosystem: implications for species of conservation concern

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## ABSTRACT

**Aim** Tree-line conifers are believed to be limited by temperature worldwide, and thus may serve as important indicators of climate change. The purpose of this study was to examine the potential shifts in spatial distribution of three tree-line conifer species in the Greater Yellowstone Ecosystem under three future climate-change scenarios and to assess their potential sensitivity to changes in both temperature and precipitation.

**Location** This study was performed using data from 275 sites within the boundaries of Yellowstone and Grand Teton national parks, primarily located in Wyoming, USA.

**Methods** We used data on tree-line conifer presence from the US Forest Service Forest Inventory and Analysis Program. Climatic and edaphic variables were derived from spatially interpolated maps and approximated for each of the sites. We used the random-forest prediction method to build a model of predicted current and future distributions of each of the species under various climate-change scenarios.

**Results** We had good success in predicting the distribution of tree-line conifer species currently and under future climate scenarios. Temperature and temperature-related variables appeared to be most influential in the distribution of whitebark pine (*Pinus albicaulis*), whereas precipitation and soil variables dominated the models for subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). The model for whitebark pine substantially overpredicted absences (as compared with the other models), which is probably a result of the importance of biological factors in the distribution of this species.

**Main conclusions** These models demonstrate the complex response of conifer distributions to changing climate scenarios. Whitebark pine is considered a 'keystone' species in the subalpine forests of western North America; however, it is believed to be nearly extinct throughout a substantial portion of its range owing to the combined effects of an introduced pathogen, outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae*), and changing fire regimes. Given predicted changes in climate, it is reasonable to predict an overall decrease in pine-dominated subalpine forests in the Greater Yellowstone Ecosystem. In order to manage these forests effectively with respect to future climate, it may be important to focus attention on monitoring dry mid- and high-elevation forests as harbingers of long-term change.

**Keywords**

**Biophysical variables, climate change, climate variability, Greater Yellowstone Ecosystem, *Pinus albicaulis*, random forest model, species distribution, tree-line conifer distributions.**

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## INTRODUCTION

Anomalous warming in the late 20th century (relative to previous centuries) has been documented (National Research Council, 2006) and is anticipated to increase in the future (Intergovernmental Panel on Climate Change (IPCC), 2007). Whereas species respond to warming in distinct ways that are dependent upon their individual life histories, non-migratory species often shift their geographical ranges, and evidence of such changes is emerging on the global scale (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006). In addition, palaeoecological studies have documented individualistic responses of numerous taxa in the form of modifications of their spatial distributions, and future projections indicate that shifts in species ranges might need to occur at unprecedented rates to match predicted changes in climatic variables (Davis & Zabinski, 1992; Whitlock, 1993; Bartlein *et al.*, 1997; Davis & Shaw, 2001).

Understanding the relationship between the distribution of vegetation and biophysical variables has been an integral part of biogeographical studies, and a better understanding of these relationships will improve our ability to predict future ecological responses to climate change (Brown, 1994; Bartlein *et al.*, 1997; Iverson & Prasad, 1998; Cairns, 2001; McKenzie *et al.*, 2003; Bunn *et al.*, 2005; Norris *et al.*, 2006). Species distribution models (also called bioclimatic envelope or environmental niche models) have become an increasingly common method for describing the influence of current and future climate on the distribution of species (e.g. Bartlein *et al.*, 1997; Iverson & Prasad, 1998; Hannah *et al.*, 2002; McKenzie *et al.*, 2003; Lawler *et al.*, 2006; Prasad *et al.*, 2006). By 'training' a model on current species distributions and bioclimatic parameters, and assuming a static relationship between climate and vegetation in the future, predictions of future changes in distributions under various climatic regimes can be developed (Hannah *et al.*, 2002). These models detail species-specific responses to changes in climatic parameters and increase understanding of the physiological processes controlling current and future species distributions.

The upper tree line represents a dynamic equilibrium between climate and vegetation, and trees in these ecosystems are under tremendous environmental stress, which can be greatly amplified or moderated by small changes in temperature or precipitation (Lloyd & Graumlich, 1997; Cairns, 2001; Lloyd & Fastie, 2002). Because the tree line is believed to be limited worldwide by temperature, species inhabiting this ecotone are expected to be sensitive to temperature increases (Tranquillini, 1979; Rochefort *et al.*, 1994; Körner, 1998; Bassman *et al.*, 2003; Smith *et al.*, 2003; Körner & Paulsen, 2004). In addition to the effect of temperature, recent studies have shown that precipitation influences species establishment in this ecotone (Germino *et al.*, 2002; Daniels & Veblen, 2004).

With its relative lack of human influences (such as, for example, land-use changes and hydrological diversions), the upper tree line is an ideal place to examine the impacts of climate on conifer species. US national parks include extensive alpine and subalpine habitats, and therefore provide substantial areas of non-impacted land on which to conduct studies of future change. With the addition of the Inventory and Monitoring Program (I&M), the US National Park Service has expanded its efforts to understand the impacts of climate variability on park resources.

Our objective in this study was to improve understanding of the relationship between conifer species that comprise the upper tree line in Yellowstone (YELL) and Grand Teton (GRTE) national parks and biophysical controls on their distribution. Specifically, we focus on three conifer species that occupy the tree line in the national parks of the Greater Yellowstone Ecosystem: whitebark pine (*Pinus albicaulis* Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). It was the goal of this study to focus specifically on the tree line within park boundaries in order to define the relationship between bioclimatic variables and the spatial distribution of high-elevation species within the parks. We also focused on using publicly available data on bioclimatic variables in order to present the model as an example of a low-cost method for incorporating climate-change scenarios into natural resource management. The inclusion of ecosystem drivers and their effects on ecosystem function is especially important for natural resource management in protected areas, such as national parks, owing to the limitations of stationary political boundaries and the subsequent impacts of these boundaries on the management of natural resources across large ecosystems that encompass numerous land-management agencies (Halpin, 1997).

The practical use of biophysical envelope models for describing current and future distributions of species may be limited because these models do not incorporate biotic interactions among species, dispersal ability, evolutionary change, disturbance or herbivory (Pearson & Dawson, 2003; Cairns & Moen, 2004; Guisan & Thuiller, 2005; Araújo & Guisan, 2006). Furthermore, bioclimatic models are generally built using the realized niche of the species (e.g. where it is currently located across the landscape, which incorporates biotic interactions), whereas they predict the fundamental niche of the species [e.g. where the environmental conditions are suitable for survival and reproduction (Pearson & Dawson, 2003; Peterson, 2003; Guisan & Thuiller, 2005; Thuiller *et al.*, 2005; Whittaker *et al.*, 2005; Araújo *et al.*, 2006; Pearson *et al.*, 2007)]. These models also assume that equilibrium conditions exist between climate and vegetation and that these conditions can be applied to future climate–vegetation relationships (Woodward & Beerling, 1997; Davis *et al.*, 1998; Pearson & Dawson, 2003). However, the degree to which species are in equilibrium with their environment is variable and often unknown (Guisan & Thuiller, 2005), although it may be assumed that upper tree-line conifer species are not in equilibrium with their environment, as they often demonstrate lagged response times to environmental change as a result of slow growth rates and limited dispersal (Lloyd & Graumlich, 1997; Körner, 1998). In addition to the aforementioned theoretical limitations, it is important to take into account that a model developed using the observed distribution of a species, while providing information that helps to define its current environmental requirements, does not provide information on all possible combinations of environmental variables that could occur, especially in the future under changing climate scenarios (Jackson & Overpeck, 2000). Moreover, while these models are ideally built using the entire range of the species, envelopes that incorporate only a portion of the range of the species can provide useful information in certain situations. For instance, the degree of subspeciation and genetic distance is understudied in subalpine forests, and some studies suggest that gene flow in subalpine forests is limited (Grant & Mitton, 1977). If this is the case in our study system, there is a good argument for limiting the geographic range of the envelope, as we have done in this study. Although constraints exist on the applicability of niche models and the results of such models must be interpreted with caution, species distribution models can provide important biogeographical information about species (Pearson *et al.*, 2007), and the principle behind using a biophysical envelope to describe current and future species distributions has been supported in comparative studies (Martínez-Meyer *et al.*, 2004; Thuiller *et al.*, 2005).

Two previous studies have explored the use of biophysical envelope models for projecting the impact of future climate change on forests in the Yellowstone region. Romme & Turner (1991) conceptually examined the consequences of three possible future climate scenarios on the spatial extent and elevation of forest zones in the Greater Yellowstone Ecosystem. In addition, Bartlein *et al.* (1997) examined the potential future distributions of various tree species within the Yellowstone region using a coarse-resolution climate model to understand the impact of doubling of carbon dioxide on species ranges. We contend that focusing this study on long-lived upper tree-line conifer species and using a robust statistical technique that has strong predictive power exploits the positive aspects of species distribution modelling and minimizes the downfalls of the technique. In this study, our objectives were to examine the potential shifts in spatial distribution of three tree-line conifer species in the Greater Yellowstone Ecosystem under three future climate-change scenarios and to assess the potential sensitivity of each species to changes in temperature and precipitation.

## METHODS

### Study area

YELL and GRTE comprise the core of the Greater Yellowstone Ecosystem. Together, they represent approximately one million hectares of reserves straddling the Wyoming, Montana and Idaho borders. YELL is dominated by a relatively flat volcanic plateau, with three major mountain ranges bordering the plateau, which provide high-elevation subalpine and alpine habitats. The presence of two topographically distinct areas has led to the description of two major climates for YELL, with the highest temperatures and lowest precipitation occurring in the large valleys of the northern portion of the park, and lower temperatures and higher precipitation occurring in the south-western corner of the plateau (Despain, 1987; Whitlock & Bartlein, 1993). GRTE also encompasses a wide variety of topography, including the Teton Range and numerous hectares of riparian corridors and morainal lakes. Most of the precipitation for high-elevation areas in both parks is contained within the annual snowpack, which can reach five to ten metres during heavy snowfall years (National Park Service (NPS), 2006).

Soils in the Yellowstone region are highly influenced by the volcanic history of the region. Most soils found on lower-elevation plateaus are rhyolites of volcanic origin, whereas higher-elevation forests and meadows are underlain by andesites (Despain, 1990). Rhyolitic soils are comparably low in nutrients (particularly calcium) and are mostly sand, whereas andesitic soils are higher in plant nutrients and are texturally dominated by clay (Despain, 1990). Thus, vegetation species that require more nutrients and deeper rooting depths are believed to preferentially inhabit andesitic sites (Despain, 1990).

### Vegetation source data

Data on the distribution of tree-line species in YELL and GRTE were obtained from the USDA Forest Service Forest Inventory and Analysis Program (FIA). The goal of FIA is to determine the amount of timber available on public and private forested lands throughout the US by regularly inventorying sample plots across the landscape (US Department of Agriculture Forest Service, 2001). Groups of four circular subplots with a radius of approximately 7 m are regularly spaced at 4.8-km intervals across all forested lands within the US, and a census of the plots is performed annually. For specific information on the sampling design used by the FIA Program, please refer to the FIA field guide (USDA Forest Service, 2001).

Plot-level data obtained for this study included the geographic coordinates of each plot, topographic variables (including elevation, slope and aspect) and the number and size of all trees with a diameter at breast height (dbh) > 2.5 cm (where dbh is measured at 1.37 m above the ground). We converted species abundance data (i.e. dbh and number of stems of each species) to presence/absence values associated with each of the FIA plot locations. From these data, a GIS layer showing the location of each of the sample plots was developed using ArcMap 9.1 (Fig. 1; Environmental Systems Research Institute (ESRI), Inc., 2005).

### Climate data

Climatic parameters were obtained from the DAYMET climate model, which uses spatial interpolation techniques and raw weather-station data to account for variations in climate across the landscape resulting from topography and elevation

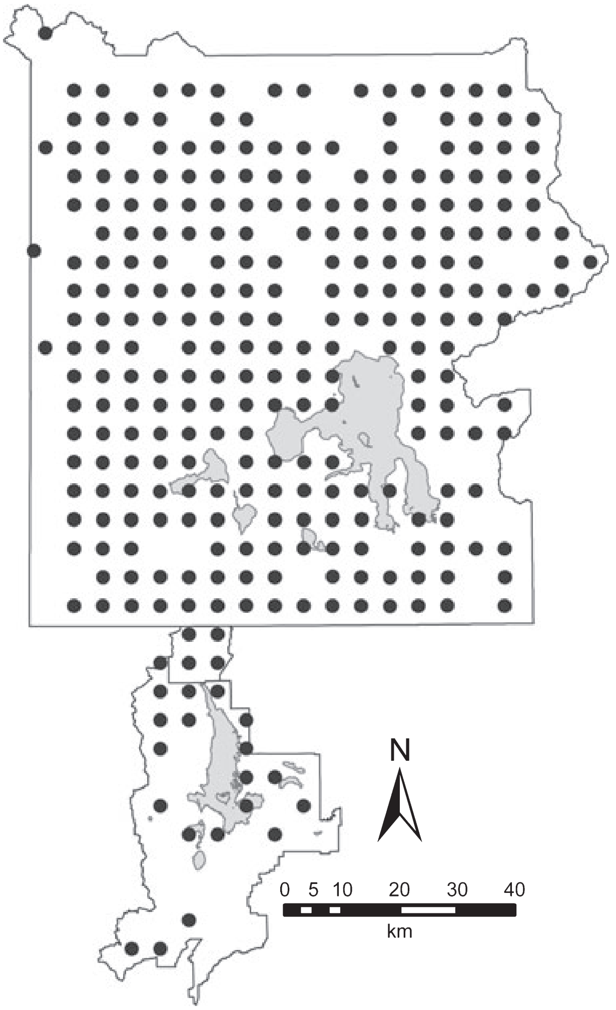

**Figure 1** Map of the spatial distribution of USDA Forest Service Forest Inventory and Analysis plots (locations represented by black dots) from which data were used for the study.

(Thorton *et al.*, 1997). Values for various climatic parameters are calculated for remote locations using extrapolation techniques that incorporate elevation-dependent lapse rates for temperature variables and total annual precipitation and the frequency of precipitation events for precipitation variables (Thorton *et al.*, 1997). Net solar radiation is calculated as a function of the relationship between daytime temperature range and cloud cover (Bristow & Campbell, 1984). Mean values for the period 1980–1997 for 20 variables (Table 1) were downloaded as grids at a 1-km resolution and clipped to the geographic extent of the study area. Although the use of climate data at this spatial resolution is not ideal for model building at this scale, we believe that it provides more accurate estimates of climatic parameters than would the use of raw data from weather stations that are often located at much lower elevations and many kilometres from site locations. We then overlaid the vegetation plots on the DAYMET grids and extracted the values for the climatic variables at each of the plot locations.

**Table 1** Bioclimatic parameters used as predictor variables in the models. Climate variables represent the mean value over the 18-year period from 1980 to 1997 at a 1-km scale. Data are from Thorton *et al.* (1997) and Miller & White (1998).

| Climate variables | Soil variables |
|---|---|
| Average air temperature | Depth to bedrock |
| Daily maximum temperature | Bulk density for 11 layers |
| Daily minimum temperature | Hydrological soil group (4 groups) |
| Maximum summer (JJA) temperature | Porosity for 11 layers |
| Maximum winter (DJF) temperature | Rock fragment texture for 11 layers |
| Minimum summer (JJA) temperature | Rock fragment volume for 11 layers |
| Minimum winter (DJF) temperature | Sand, silt and clay fraction for 11 layers |
| Average summer (JJA) temperature | Soil texture for 11 layers |
| Average winter (DJF) temperature | Available water capacity at 100, 150 and 250 cm depth |
| Maximum July temperature | |
| Maximum January temperature | |
| Minimum July temperature | |
| Minimum January temperature | |
| Total annual precipitation | |
| Total winter precipitation | |
| Total summer precipitation | |
| Daily average water vapour pressure | |
| Frost days | |
| Growing degree days | |
| Daily total shortwave radiation | |

## Soil data

Soil data were derived from CONUS-SOIL digital soil maps, based on data from the USDA Natural Resources Conservation Service as part of the State Soil Geographic Database program, which uses a minimum map unit of 1.25 km (Miller & White, 1998). The goal of the CONUS-SOIL data set is to provide soil data for GIS-based analyses in a systematic format across the continental US. Interpolation of raw soil data was accomplished by determining the approximate coverage of each soil property within each 1-km cell and using weighted averages to assign a value for each soil property to each cell. Eleven variables (Table 1) that describe the texture, water-holding capacity and depth of the soil were used (Miller & White, 1998). Raster data sets at a 1-km resolution were downloaded and clipped to the study area, and soil variables were extracted for each of the vegetation plot locations.

## Future climate scenarios

Future climate predictions for species distribution modelling are generally derived from general circulation models (GCMs); however, the applicability of these models at a regional scale has been questioned owing to their coarse resolution (Bartlein *et al.*, 1997; Mearns *et al.*, 2003). We therefore chose to examine the sensitivity of tree-line species to possible changes in climate using one scenario of potential future climate that falls within the range of climate variables predicted by GCMs for the Northern Rockies and Yellowstone region (e.g. Bartlein *et al.*, 1997; Hansen *et al.*, 2001). This model was used to predict the future distribution of each species under three climate-change scenarios: (1) an increase in temperature by 4.5°C and an increase in precipitation by 35%; (2) an increase in temperature by 4.5°C only; and (3) an increase in precipitation by 35% only. Theoretically, these three scenarios demonstrate the individual effects of changes in temperature and precipitation on species distributions as well as the combined effect of changes in both variables, thus allowing us to conduct an analysis of the sensitivity of the tree-line system to changes in these parameters. Based on warming rates observed during the past century (National Research Council, 2006) and future projected changes (Hansen *et al.*, 2001), this scenario serves as a conservative estimate of possible future changes in the region.

### Data analysis

All analyses were performed in the R 2.3.1 statistical environment (R Core Development Team, 2005). We used the random forest prediction method for understanding current and future relationships between vegetation distribution and climatic and soil parameters. Random forest is a recently developed modelling technique that is based on classification (and regression) tree analysis (CTA; Breiman, 2001). Owing to their hierarchical nature, random forest and CTA are capable of capturing non-linear relationships in predictor variables and can be particularly useful with climate and soil variables, which often exhibit complex interactions. However, random forest departs from CTA by developing hundreds to thousands of classification trees, with each tree built using a random subset of the data and a randomly chosen suite of predictor variables at each node. The trees are then aggregated. Thus, models tend to have more stable error rates, whereas CTA is highly influenced by minor variations in the data (for example, different random subsets of samples often produce substantially different models). Few parameters in the random forest model can be manipulated (i.e. the number of trees grown, the number of variables to try at each split), and the outcome is not very sensitive to modifications of these parameters. We optimized the number of classification trees grown (1000) and predictor variables tried at each split (93, or 66%) to minimize the 'out-of-bag' (OOB) error estimate [described below (Liaw & Wiener, 2002)]. No overfitting of trees – a common occurrence in CTA – occurs when using random forest. Thus, random forest is a useful modelling method for making future predictions (Prasad *et al.*, 2006).

Random forest provides an out-of-bag (OOB) error estimate, which is calculated as an error rate based on the samples that are withheld from the analysis. Therefore, it might be unnecessary to split data sets into 'training' and 'testing' subsets, which is advantageous with small data sets (Liaw & Wiener, 2002; Lawrence *et al.*, 2006) such as the initial FIA data set used in this study. Because random forest is a relatively new analysis technique, however, we compared the error rates for the model using the entire data set and a random subset of the data (e.g. a 50–50 split) used for training and testing the model. These results showed that error rates were very similar among the models, with differences ranging from 0.09% to 2.19% (Table 2). We thus chose to use the full data set for model building. We used the model developed in random forest to predict the presence or absence of tree-line conifer species for each of the 1-km raster cells within the boundaries of YELL and GRTE under current conditions and each of the three future climate scenarios.

**Table 2** Error rates (percentage of cells incorrectly classified) for the current species distribution models using the full and split data sets.

| | Subalpine fir ($n$ = 157) | Engelmann spruce ($n$ = 119) | Whitebark pine ($n$ = 56) |
|---|---|---|---|
| Full dataset ($n$ = 275) | 33.45 | 33.81 | 23.27 |
| Training data set (50%) | 33.57 | 34.31 | 23.36 |
| Testing data set (50%) | 35.04 | 32.11 | 23.36 |

We used variable importance plots to explore more closely the relationship between the predictor variables and the distribution of the species. Random forest determines the importance of a predictor variable by calculating the increase in prediction error when the OOB samples for that variable undergo permutation while all other predictor variables are held constant (Liaw & Wiener, 2002). In practice, variable importance is plotted as the mean decrease in accuracy of the model when the aforementioned process is carried out for each predictor variable (Fig. 2). Interpretation of these plots is hindered by the intercorrelation and autocorrelation among the predictor variables. Thus, the importance of each variable should be interpreted cautiously and in relation to its interaction with the other predictor variables.

To determine if the classifications performed better than a random expectation, we used the Kappa statistic. Kappa statistics are indices that account for chance agreement that may occur if values are randomly assigned to each cell across the landscape. Thus, comparing the actual and chance agreement, along with the associated $P$-values, allowed us to assess the degree to which the model correctly predicted presence and absence values compared with a random classification (Congalton & Green, 1999).

## RESULTS

### Model results

The models showed a decrease in the percentage of plots occupied by all tree-line species when the temperature

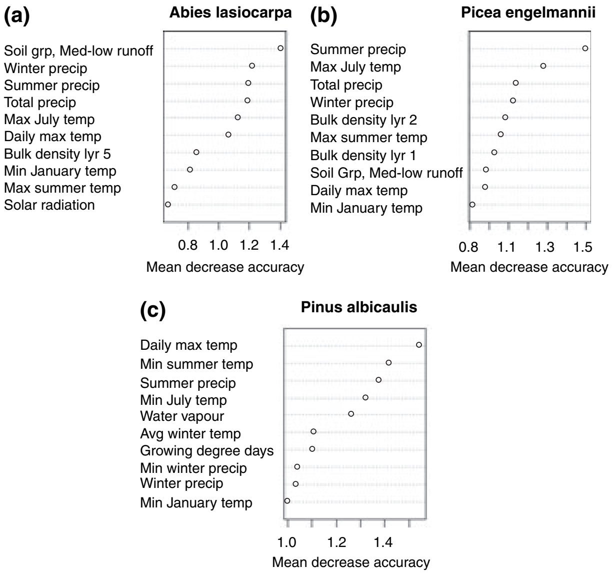

**Figure 2** Variable importance plots for subalpine fir (a), Engelmann spruce (b) and whitebark pine (c). Variable importance plots represent the overall percentage mean decrease in accuracy of the model when each of the 10 variables shown is permuted while all other predictor variables are held constant.

**Table 3** Percentage of area predicted to be occupied by tree-line species under four climate scenarios.

| | Subalpine fir | Engelmann spruce | Whitebark pine |
|---|---|---|---|
| Current climate | 42.56 | 28.69 | 12.18 |
| Increased temperature | 14.13 | 2.98 | 0.02 |
| Increased precipitation | 52.80 | 30.66 | 13.02 |
| Increased temperature and precipitation | 17.28 | 5.02 | 0.02 |

increases (Table 3). All species showed an increase (albeit slight for whitebark pine and Engelmann spruce) with increased precipitation. Increasing both parameters led to a decrease in all species.

The random-forest package allowed for the development of plots that showed the relative importance of each of the predictor variables to the model. The following predictor variables were most influential in model building: hydrological soil group b, which refers to soils with moderate infiltration capacities, for subalpine fir; summer precipitation for Engelmann spruce; and average daily maximum temperature for whitebark pine (Fig. 2). Whereas climatic variables dominated the models for all species, soil variables played a more important role for spruce and fir than for whitebark pine (Fig. 2). The variable importance plot showed that bulk density, a measure of the water retention potential of the soil, of the uppermost soil layers [approximately 10 cm (Miller & White, 1998)] was important for distinguishing the location of Engelmann spruce stands. However, subalpine fir was more directly impacted by the bulk density of lower layers (layer 5, which occurs at 30–40 cm depth), as well as by the fraction of clay in the soil at greater depths (Fig. 2).

## Model evaluation

Model evaluation results suggested that the random-forest prediction method was able to identify current species distributions with a level of accuracy ranging from 66.55% for the model of subalpine fir distribution to 76.73% for the model of whitebark pine distribution. The three random-forest models had a level of accuracy between 66% and 77% (Table 2). Overall error rates were lower for the whitebark pine model than for models for Engelmann spruce and subalpine fir. The inability to differentiate microsite conditions at a 1-km scale probably contributed to the difficulty in predicting the locations of spruce and fir, which commonly co-occur.

The capacity of the model to distinguish correctly between occupied and unoccupied sites is another important aspect of model evaluation (Guisan & Zimmerman, 2000). Confusion matrices are commonly used in assessing the accuracy of classifications in a variety of fields, such as remote sensing, and quantify the level of agreement (or disagreement) between the input data and model predictions (Lillesand & Keifer, 1999). We used confusion matrices to calculate class error rates for unoccupied sites that were classified as occupied (e.g. errors of commission) and for occupied sites that were classified as unoccupied (e.g. errors of omission). Full results are shown in Table 4. Kappa statistics suggested that all three models classified presence and absence of tree-line species more accurately than a random classification (subalpine fir: $\kappa = 0.31$, $P < 0.0001$; whitebark pine: $\kappa = 0.15$, $P = 0.01$; Engelmann spruce: $\kappa = 0.31$, $P < 0.0001$). However, omission errors were particularly high for whitebark pine. Likely explanations for these errors are outlined in the discussion section, and caution should be used when interpreting the results of these models.

## Mapped results

An important goal of the biogeographical modelling used here is to understand the spatial changes in tree-line conifer distributions that could occur under various future climate scenarios. We thus mapped current and future distributions of tree-line conifer species across YELL and GRTE to determine changes in the spatial distributions of these species. Changes in the proportion of the landscape occupied by each species in

**Table 4** Commission and omission error rates (percentage of cells incorrectly classified).

| | Subalpine fir | Engelmann spruce | Whitebark pine |
|---|---|---|---|
| Commission | 41.53 | 29.49 | 9.13 |
| Omission | 27.39 | 39.50 | 78.57 |

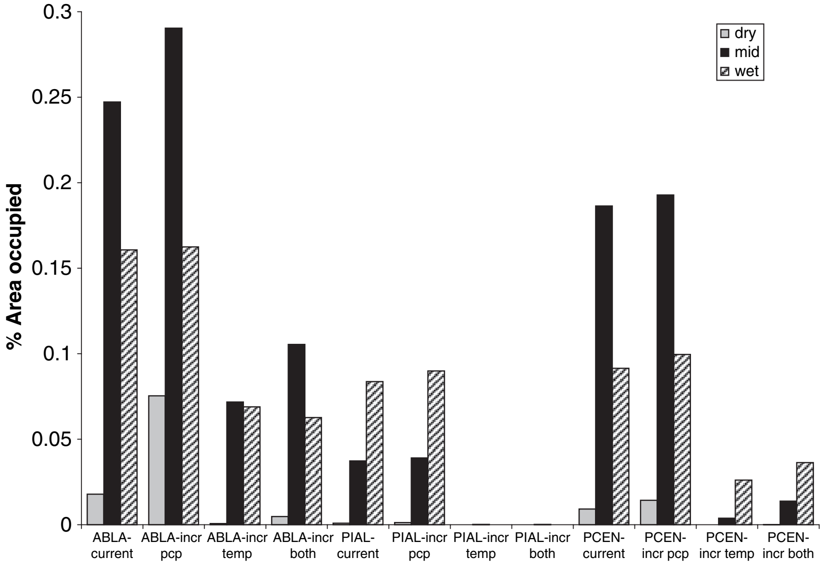

**Figure 3** A bar graph representing the percentage of area occupied by each species under the four climate scenarios in three moisture zones (dry, middle, wet). Moisture zones were defined by dividing the total annual precipitation within park boundaries into quartiles and using the following classifications: dry = >39–77 mm; middle = >77–104 mm; and wet = >104–208 mm.

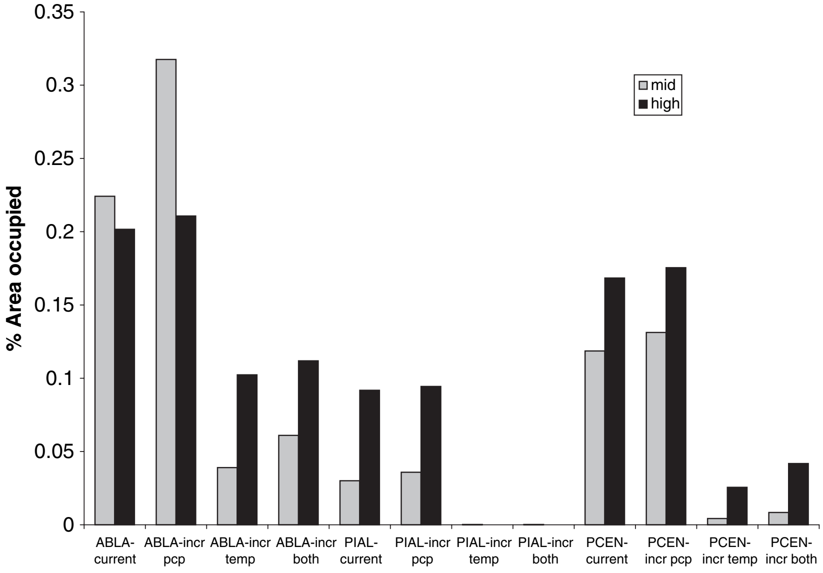

**Figure 4** A bar graph representing the percentage of area occupied by each species under the four climate scenarios in two elevation zones (middle, high). Elevation zones were determined by the elevational range within the park boundaries and the autecology of the species, with the middle-elevation zone representing all areas ≤ 2590 m and the high-elevation zone representing all areas > 2590 m.

three moisture zones [dry (> 39–77 mm), middle (> 77–104 mm), and wet (> 104–208 mm)] and two elevation zones [middle (≤ 2590 m) and high (> 2590 m)] were calculated (Figs 3 & 4).

If temperature and precipitation increase, subalpine fir is predicted to decrease in mid- and high-elevation areas and to be present primarily in the highest-elevation and wettest mid-elevation regions (Fig. 5d). If only temperature increases, subalpine fir decreased in mid- and high-elevation areas and was present mainly in higher and wetter habitats (Fig. 5c). Subalpine fir experienced a substantial decrease in dry, high-elevation areas, such as northern YELL, with drought-like conditions (Fig. 5c). With an increase in precipitation, subalpine fir is expected to increase, mostly in wet mid-elevation regions (Fig. 5b).

Engelmann spruce showed a decrease in mid- and high-elevation regions with increased temperature and precipitation, and was mostly present at the highest elevations (Fig. 6d). With increased temperature only, Engelmann spruce showed a similar response, decreasing at all elevations and in all moisture classes (Fig. 6c). Increased precipitation led to a slight increase in the percentage of area occupied, but a relatively unchanged distribution compared with the current distribution (Fig. 6b).

Whitebark pine nearly disappeared from the park with a scenario of increases in both temperature and precipitation and a scenario of only increased temperature (Figs 7c,d). The distribution remained relatively unchanged with an increase in precipitation (Fig. 7b).

## DISCUSSION

These models demonstrate the complex response of conifer distributions to changing climate scenarios. Under a scenario

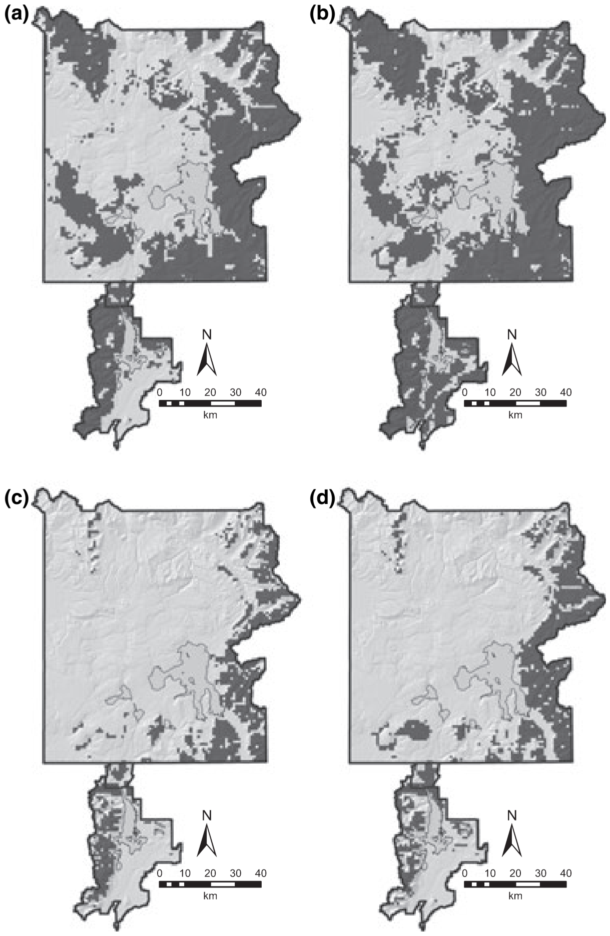

**Figure 5** Distribution of subalpine fir (dark shading) under (a) current climatic conditions, (b) a scenario of increased precipitation by 35%, (c) a scenario of increased temperature by 4.5°C, and (d) a scenario of increased temperature by 4.5°C and precipitation by 35%.

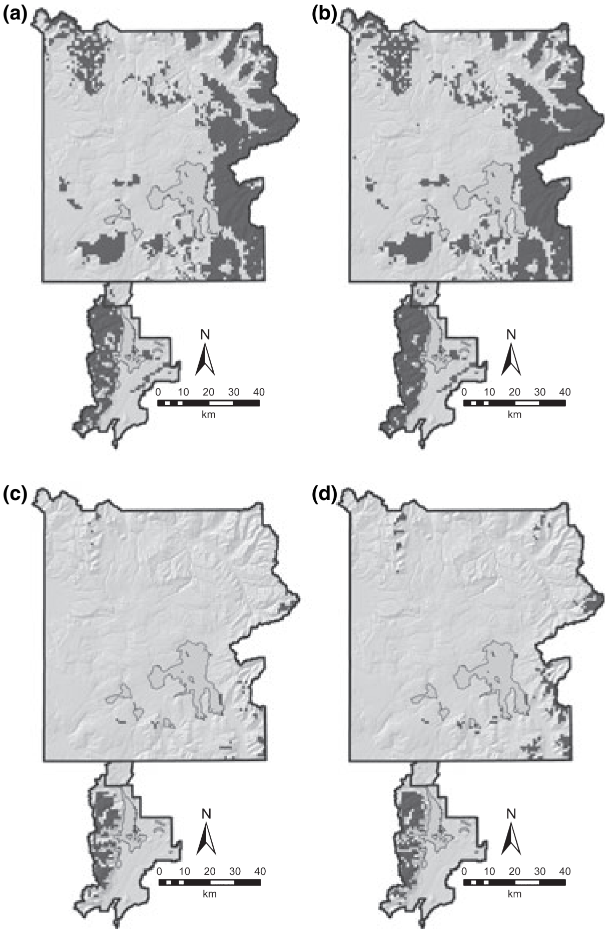

**Figure 6** Distribution of Engelmann spruce (dark shading) under (a) current climatic conditions, (b) a scenario of increased precipitation by 35%, (c) a scenario of increased temperature by 4.5°C, and (d) a scenario of increased temperature by 4.5°C and precipitation by 35%.

of increased temperature, as well as a scenario of increased temperature coupled with increased precipitation, the models showed a substantial decrease in the overall distribution of tree-line conifer species across the Yellowstone landscape. This supports the existing hypothesis that the response of long-lived, non-migratory species, such as tree-line conifers, to increased temperatures is upslope movement to higher elevations (Innes, 1991; Rochefort *et al.*, 1994; Lloyd & Graumlich, 1997; Millar *et al.*, 2004). All of the species modelled in this study inhabit the coldest and wettest forest zones (Alexander & Shepperd, 1990; Alexander *et al.*, 1990; Arno & Hoff, 1990). Because the autecology of many tree-line species prevents them from inhabiting warmer zones, the species modelled here experience a decrease in overall habitat with an increase in temperature (Tranquillini, 1979; Alexander & Shepperd, 1990; Alexander *et al.*, 1990; Arno & Hoff, 1990). In contrast, an increase in precipitation led to an increase (albeit small in the case of whitebark pine and Engelmann spruce) in the area occupied by tree-line conifers. Because these species inhabit relatively wet areas on the landscape, higher precipitation led to an increase in inhabitable mid-elevation cells that fell within the temperature requirements of the species. Whitebark pine, as a true subalpine species, is found near the summits of most peaks in YELL and GRTE, and has only small areas of currently non-forested alpine zone into which to migrate (Despain, 1990). In addition, physical factors such as wind and drifting snow can prevent the establishment of individual trees above the current tree line, even if climate parameters are compatible with successful recruitment (Malanson *et al.*, in press). It is therefore expected that an increase in precipitation would lead to a proportionally small increase in the area occupied by whitebark pine.

Precipitation and soil variables played a larger role in the models for subalpine fir and Engelmann spruce than they did for whitebark pine. Temperature variables dominated the whitebark pine models, following the autecology of this specialized subalpine species that is heavily influenced and limited by growing-season temperature. Because Engelmann

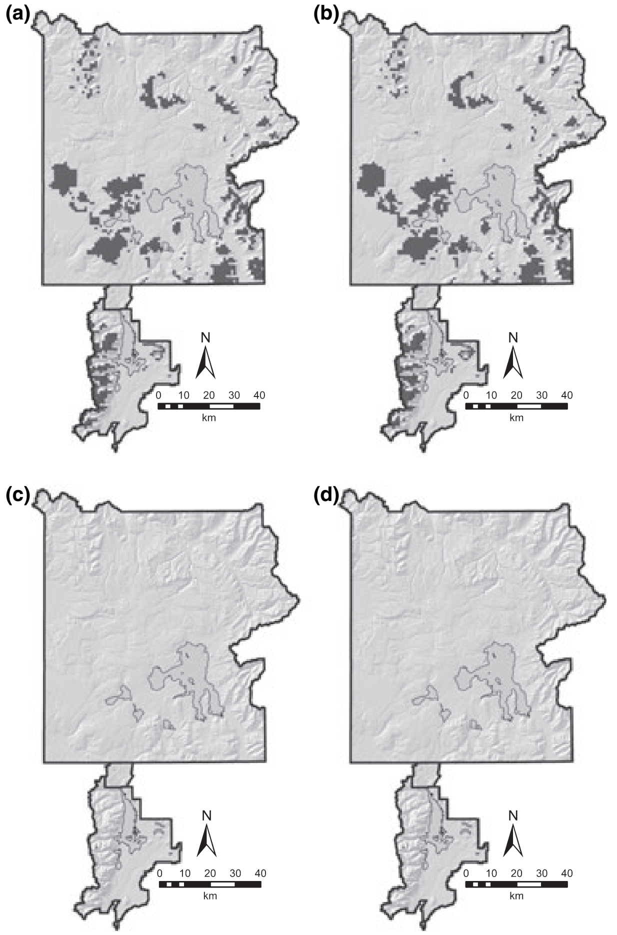

**Figure 7** Distribution of whitebark pine (dark shading) under (a) current climatic conditions, (b) a scenario of increased precipitation by 35%, (c) a scenario of increased temperature by 4.5°C, and (d) a scenario of increased temperature by 4.5°C and precipitation by 35%.

spruce is more likely to grow in areas with accessible water tables than to require specific physical soil properties, the importance of shallow bulk density is probably a reflection of its establishment on sites that provide ample water availability in the upper soil layers (Alexander & Shepperd, 1990). In contrast, according to these models, water availability at greater depths appeared to be a more important variable to subalpine fir. However, the distribution of subalpine fir is also likely to be tightly linked to competitive interactions, as it is known to establish on sites that are ''too wet or too dry for its common associates'' (Alexander *et al.*, 1990).

It should be noted that, because climate and soil variables are inherently spatially and temporally autocorrelated and the groups of variables are intercorrelated, it is difficult to interpret the importance of each variable to the model separately. It is instead more likely that groups of variables are acting together to influence the presence or absence of each species. With rapidly changing climate, the correlation among climatic and edaphic variables is likely to vary in the future. Shifts in soil fauna and microbial communities could occur in relation to changes in plant distribution, which may lead to changes in the availability of carbon and nitrogen (Hausenbuiller, 1985). However, major changes on short temporal scales are likely to result from changes in soil moisture properties, as increases in temperature will lead to earlier snowmelt runoff and, consequently, earlier soil moisture recharge, which may lead to earlier desiccation of soils (Hamlet *et al.*, 2007).

Changes in the spatial distribution of tree-line conifers were coupled with relative moisture across the Yellowstone landscape, emphasizing the importance of moisture availability to tree-line composition and structure. The influence of moisture on tree-line dynamics has long been overlooked in long-term, large-scale studies in favour of examining the effects of increased temperature, as the tree line is believed to be controlled by temperature worldwide (e.g. Tranquillini, 1979; Innes, 1991; Körner, 1998; Camarero & Gutiérrez, 2004; but see Daniels & Veblen, 2004). For instance, under drought-like conditions, high elevations in YELL and GRTE became dominated by spruce–fir forests, with a decrease in the area occupied by whitebark pine. With an increase in precipitation, the probability of occurrence of all tree-line species increased across the landscape. However, whereas the spatial distributions of Engelmann spruce and whitebark pine remained relatively unchanged, subalpine fir increased in the wettest mid-elevation areas. Thus, the spatial implications of increased precipitation were an increase in fir-dominated forests in the wettest mid-elevation areas, which could lead to the replacement of whitebark pine in mid-elevation, mixed-conifer forests.

The models for whitebark pine substantially under-predicted presences (i.e. high omission error rates), and caution should be used when interpreting current and future distribution maps. Possible explanations for these error rates are probably based on the biology of this species and the interaction between climate and multiple factors driving its distribution across the landscape. For example, it is the only one of the three species that is dispersed by animals instead of wind. Clark's nutcrackers (*Nucifraga columbiana*) tend to disperse whitebark pine seeds in open areas and on ridges (Tomback *et al.*, 2001), and, as such, whitebark pine is often found on sites that may not be climatically optimal, but on which it can establish. Furthermore, significant dieback of whitebark pine stands in the Greater Yellowstone Ecosystem and beyond is occurring owing to white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*) and changing fire regimes. Thus, mortality rates are probably higher than they would be under normal circumstances due to these factors, which makes predicting the distribution of whitebark pine using only climatic and soil variables difficult. In addition, climate, fire, mountain pine beetle outbreaks and blister rust infection are interrelated processes, and these relationships are integral to understanding the distribution of this species and should be incorporated into future distribution models. Thus, it is evident that a first-order, process-based model for this system is inadequate and that biology is likely to play an important role in whitebark pine distribution. Therefore, the introduction of meta-population dynamics (Dobson, 2003) to explain dispersal mechanisms and disturbance models to integrate factors driving high mortality rates is extremely important for future modelling efforts. The models of present-day distribution, however, should be interpreted with caution, and models of future distribution of whitebark pine distribution probably under-represent the species on the landscape.

### Management implications

Existing models have emphasized the impact of the following processes on tree-line forest dynamics: changing fire regimes and their impact on successional pathways owing to fire suppression practices in the 20th century (e.g. Keane, 2001; Kipfmueller & Kupfer, 2005); increased infestations by introduced pathogens (Koteen, 2002); more frequent and intense outbreaks of native pests (Logan & Powell, 2001; Logan *et al.*, 2003; Logan & Powell, 2005); and herbivory (Cairns & Moen, 2004). However, few studies have emphasized the importance of the direct impact of climate on tree line conifers – especially whitebark pine – in the region (exceptions include Romme & Turner, 1991; Bartlein *et al.*, 1997).

Whitebark pine is considered a ‘keystone’ species in the subalpine forests of western North America (Arno & Hoff, 1990; Tomback *et al.*, 2001). Its large seeds are high in fat and provide an important food source to seventeen animal species throughout its range – most notably the grizzly bear, a species of conservation concern (Tomback *et al.*, 2001). However, it is believed to be ‘‘functionally extinct in more than a third of its range’’ (Tomback *et al.*, 2001) as a result of the combined effects of white pine blister rust, an introduced pathogen, outbreaks of the native mountain pine beetle and changing fire regimes (Kendall, 2003).

The current study highlights the impact of a changing climate on the tree-line forests of the Yellowstone region, which in some areas are currently dominated by whitebark pine. Given future predicted changes in climate, it is reasonable to predict an overall decrease in pine-dominated subalpine forests in YELL and GRTE. However, of greater importance to land managers is the implication that whitebark pine is likely to decrease in the driest mid- and high-elevation forests in northern and central YELL – the areas in which it is currently dominant (Despain, 1990; McCaughey & Schmidt, 2001). From a forest ecology perspective, a loss of high-elevation whitebark pine forests in northern Yellowstone would lead to an overall decrease in genetic diversity and loss of subalpine habitat connectivity. This change would, in turn, have an impact on species that are dependent on whitebark pine, including animal species such as Clark’s nutcrackers (the primary seed-dispersal agent for whitebark pine) and grizzly bears, and understorey plant communities, which rely on the open-grown canopies that are typical of whitebark pine stands (Bassman *et al.*, 2003).

However, from the perspective of ecosystem management, especially in relation to the threatened grizzly bear, the predicted loss of mid-elevation, mixed-pine forests in drier areas of the ecosystem might be of greatest management importance. Mixed whitebark pine forests are highly valuable to grizzly bears because they provide more suitable habitat than monotypic stands for red squirrels, which harvest the cones from whitebark pines and cache them in middens (Mattson & Reinhart, 1997). Grizzly bears then dig up middens to find whitebark pine seeds. Without these forests, whitebark pine seeds become unavailable as a food source for grizzly bears, causing the bears to move to lower elevations to find alternative food sources (Mattson *et al.*, 2001). As grizzlies move to lower elevations, they are more likely to experience conflicts with humans (Mattson *et al.*, 2001). Thus, to manage the subalpine forests of YELL and GRTE most effectively in the face of a changing climate, it is perhaps most important to focus attention on monitoring dry mid- and high-elevation forests in the Yellowstone region as harbingers of long-term change in the ecosystem.

## CONCLUSIONS

The results of this modelling exercise suggest a possible change from pine-dominated, high-elevation forests in the Yellowstone region to spruce-fir-dominated forests. In a system that has already experienced a shift from whitebark pine-dominated forests to spruce–fir complexes (Bassman *et al.*, 2003), it is worth noting that the changes modelled in this study might exacerbate this shift and could lead to further decreases in whitebark pine. While this result alone might cause heightened concern for species of conservation concern in the Greater Yellowstone Ecosystem, it is important also to consider that the influence of other large-scale ecosystem drivers might provide additional threats to these resources. To predict the future status of these species with the greatest possible accuracy, it is necessary to couple the results of a climate model such as the one employed in this study with an enhanced understanding of the impacts of land-use change (e.g. Hernandez, 2004), shifting fire cycles (e.g. Keane, 2001), introduced pathogens (e.g. Koteen, 2002) and native pests (e.g. Logan *et al.*, 2003) on habitat availability. Only then can natural resource managers implement appropriately well-informed management practices.

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