Title

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# Abstract

# Highlights

# Introduction

Climate change is altering species distributions. Understanding how range shifts and population persistence is essential for adaptive management.

Species distribution models (SDMs) have been widely used to identify suitable habitats (REF) and predict species range shifts (REF) and inform management practices (REF). Most of the published SDMs use data from herbaria, species atlases, field surveys, expert range maps, and citizen science as occurrence data ([He et al., 2015](#ref-he2015WillRemoteSensing)), however more recently data from remote sensing have been used to produce SDMs ([Bradley and Mustard, 2006](#X5c32a085163f7984ef94bffa6e18a48d36b3eb2)). While remotely derived species occurrence data includes error, typically due to data acquisition and processing. Relative to atlas and herbaria data, remotely sensed species occurrence has several advantages. First, remotely sensed data provides both presence and absence data, while many of the other datasets commonly used only include species presence ([He et al., 2015](#ref-he2015WillRemoteSensing)). Further data from field surveys are often spatially biased. Third, spatially continuous data products can allow for more robust assessments of future range shifts by incorporating locations of known populations and information on dispersal distances.

Specifically our objectives are to: (1) better understand the relationships between aspen presence and climate, topographic, and edaphic factors and (2) map the area suitable for aspen under current climate conditions, and (3) project areas where aspen may expand, contract, or remain stable.

# Materials and Methods

## Study area

The study area consists of the Southern Rocky Mountains Ecoregion (SRME), an area of approximately 145,700 km2 that extends from southern Wyoming to northern New Mexico (Fig. 1. The SRME consists of rugged, topography with elevation ranging from 1450 m to above 4400 m, seven mountain ranges that largely trend north-south, and four Intermontane basins ([Drummond, 2012](#ref-drummond2012SouthernRockiesEcoregion)). The climate of the SRME is characterized by a continental climate, with hot summers (mean July maximum temperature of 24.5°C) and cool winters (mean January minimum temperatures of -12.3°C), and moderate precipitation (mean annual precipitation of 625 mm), most of which falls as snow ([Lukas et al., 2014](#ref-lukas2014ClimateChangeColorado); [Rodman et al., 2021](#ref-rodman2021EffectsBarkBeetle)). At local scales, the climate is driven by elevation gradients, the prevailing westerly winds, and the north-south orientation of the mountains. Temperature is generally greatest at low elevations, while total annual precipitation is generally greatest at higher elevations, particularly on the windward side of the Rockies ([Lukas et al., 2014](#ref-lukas2014ClimateChangeColorado)). Summer precipitation patterns exhibit a distinct latitudinal gradient, where more southern locations often receive more precipitation due to the North American Monsoon system ([Lukas et al., 2014](#ref-lukas2014ClimateChangeColorado)).

Ecosystems of the SRME correspond with topoclimatic patterns; low elevation valleys and intermountain basins are dominated by grasslands and shrublands, forest occupy intermediate elevations, while grasses, sedges, cushion plants, forbs, mosses, and lichens dominate cold, alpine elevations ([Comer, 2001](#ref-comer2001SouthernRockyMountains)). Within the ca. 55% of the SRME that is forested ([Drummond, 2012](#ref-drummond2012SouthernRockiesEcoregion)), topoclimatic variation drives tree species composition. Lower Montane forests (< 2,300 m) are generally composed of ponderosa pine (*Pinus ponderosae*) woodlands, piñon (*Pinus edulis*) and juniper (*Juniperus* spp.) woodlands, and gambel oak (*Quercus gambelii*) shrublands. Forests of the Upper Montane zone (ca. 2,300 - 2,800 m) are dominated by ponderosa pine-Douglas fir mixed conifer systems, quaking aspen, and lodgepole pine (*Pinus contorta*). Forests of the subalpine zone (ca. 2,800 m - 3,200 m) are dominated by Engelmann spruce, subalpine fir, and to a lesser limber pine (*Pinus flexilis)* and Rocky Mountain bristlecone pine (*P. aristata).* Forests dynamics across the SRME are strongly shaped by climate-sensitive disturbances, notably wildfires, outbreaks of native bark beetles, and windstorms ([Baker and Veblen, 1990](#ref-baker1990); [Peet, 1981](#ref-peet1981ForestVegetationColorado); [Veblen et al., 2000](#ref-veblen2000ClimaticHumanInfluences); [Veblen et al., 1994](#X6d15166298ccfaa854e56f5197e8b0dbab0811c)).

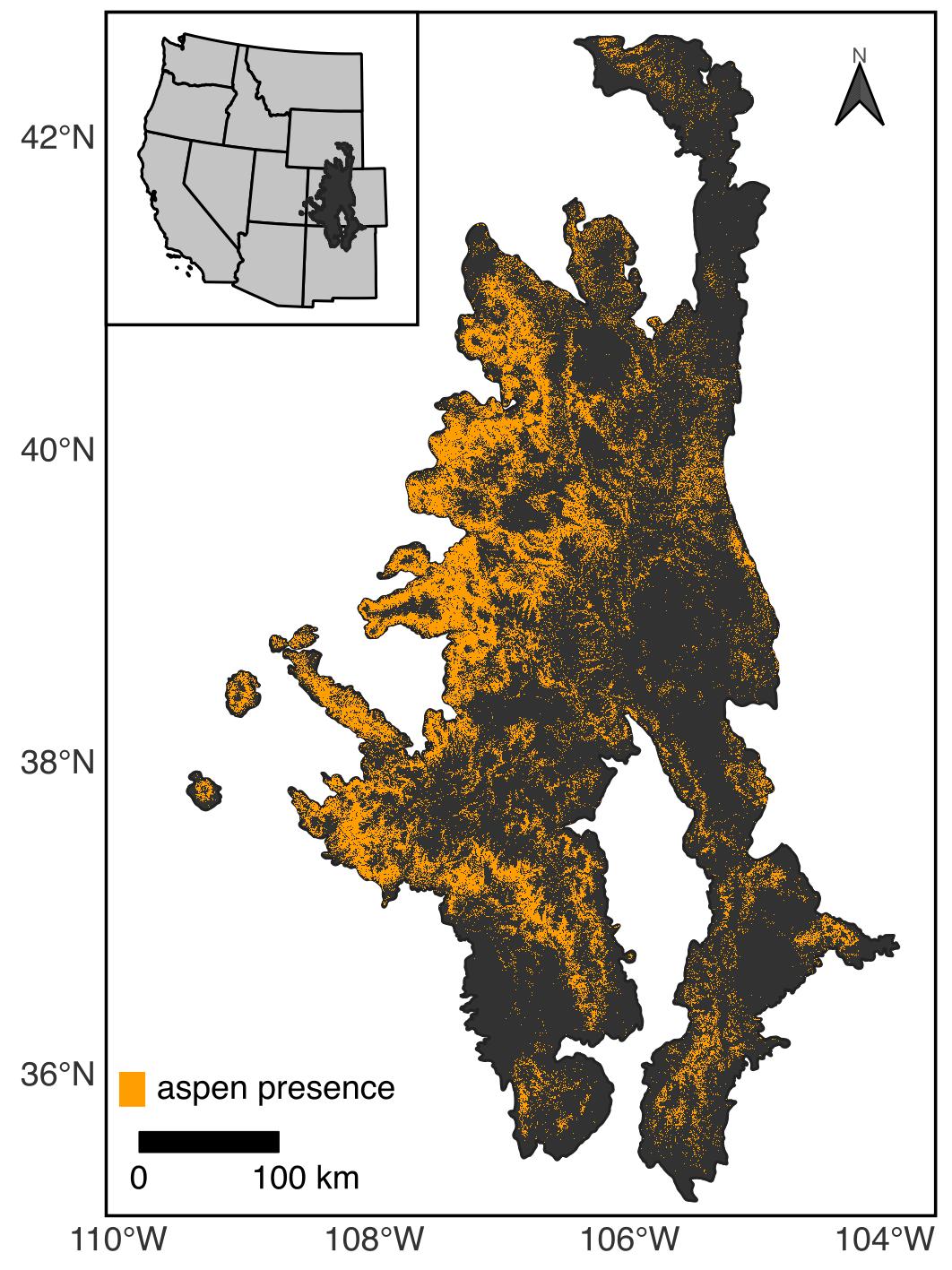


Figure 1: The Southern Rocky Mountain Ecoregion and current distribution of aspen.

## Data

### Species occurrence data

To build SDMs, we used a 10-m gridded map of aspen presence/absence produced by Cook et al. [in review]. Briefly, this dataset was produced by xyz. The map is characterized by an overall accuracy of XX.

We aggregated the data from 10-m to 90-m, a scale relevant to management ([Rehfeldt et al., 2015](#ref-rehfeldt2015)).

### Predictor variables

To understand and project the relationship between aspen and climate under historical and future conditions, we obtained gridded climate data from the AdaptWest Project ([2022](#Xcb40ace7ff505c24620413cbf7691d7f26a4667)), which provides both current and future climate data that are downscaled to 1 x 1 km resolution using the ClimateNA software (version 7.3) ([Wang et al., 2016](#ref-wang2016LocallyDownscaledSpatially)) . Current conditions, defined here as climatalogical norms for the 1981-2010 period, were generated from 4 x 4 km climate data provided by the PRISM Climate Group ([2021](#ref-prismclimategroup2021)). Future climate conditions were generated from data included in the sixth phase of Coupled Model Intercomparison Project (CMIP6). Here we used projections of future climate for the periods 2011-2040, 2041-2070, and 2071-2100. Given considerable uncertainty about future emissions, we compared two scenarios (i.e., Shared Socioeconomic Pathways; SSPs) generated under CMIP6, SSP2-4.5 and SSP5-8.5. The SSP2-4.5 scenario describes an intermediate scenario characterized by moderate increases in emission through 2040 followed by a decline, while the SSP5-8.5 scenario describes a more extreme situation where emissions increase through 2100 ([Riahi et al., 2017](#ref-riahi2017SharedSocioeconomicPathways)). In addition to uncertainty about societal decisions about greenhouse gas emissions represented in the SSPs, variation exists among the more than 50 atmosphere-ocean general circulation models (AOGCMs) included in CMIP6 due differences in complexity, assumptions, and parameterization. Thus not all AOGCMS are equally useful for regional planning purposes. For instance predictions made by some AOGCMs are believed to overestimate future warming ([Hausfather et al., 2022](#X0773c8e2ab11f078ec717d59314f0220fe06795)). Further AOCGMs differ in the number of simulations for the historical period, amount of bias, and spatial grain ([Mahony et al., 2022](#ref-mahony2022GlobalClimateModel)). Here we make use of an ensemble data constructed from eight AOCGMs identified by Mahony et al. ([2022](#ref-mahony2022GlobalClimateModel)) as being appropriate for regional applications in North America, such as species distribution modeling.

To characterize the climate space that aspen occupies, we examined 34 biologically relevant climate variables commonly used in species distribution models (Table ??. Broadly, these variables characterize the temperature, precipitation, seasonality, and interactions between precipitation and temperature. To avoid collinearity between climate predictors, we calculated pairwise correlation coefficients. When |r|>0.75, we removed variables based on existing research (Table ??. Where evidence was similar, we used univariate random forest (RF) models to evaluate the potential explanatory power of each predictor and congruence with hypothesized relationships (for more details see Appendix ??. The resulting dataset consisted of five climate variables, an annual dryness index (ADI), growing season precipitation (GSP), the ratio of GSP to degree days above 5 °C (GSPDD5), the ratio of GSP to mean annual precipitation (PRATIO), mean annual relative humidity (RH), and the difference between the mean coldest month temperature and the mean warmest month temperature (TD) (Table ??).

Given mountainous areas such as the Southern Rocky Mountains are characterized high topoclimatic variation ([Franklin et al., 2013](#ref-franklin2013ModelingPlantSpecies)), we further downscaled our selected climate variables from a 1 km resolution to a 250 m resolution using gradient and inverse distance squared (GIDS) interpolation ([Flint and Flint, 2012](#ref-flint2012DownscalingFutureClimate); [Nalder and Wein, 1998](#X44a33479d922de88fa614470bb4d0b1d1f5aa3e)), following methods outlined in Rodman et al. ([2020](#ref-rodman2020ChangingClimateSnuffing)). As ancillary data in the downscaling, we used a 30-m digital elevation model (DEM) from the USGS ([2023](#X6d15385bd2515b6b1604e69149483d60c1b1585)).

In addition to climate variables, we also included data describing terrain and soils as predictors in our models. To account for the potential effects of local topographic variation on soil transport and water balance, we use the DEM to calculate the topographic position index [TPI; Weiss ([2001](#ref-weiss2001))]. We calculated TPI for a 3-cell neighborhood (TPI3) to characterize fine scale topographic patterns ([Rodman et al., 2020](#ref-rodman2020ChangingClimateSnuffing)). To account for the effects of aspect and slope on microclimate, we calculated the Heat Load Index [HLI; McCune and Keon ([2002](#ref-mccune2002EquationsPotentialAnnual)); McCune ([2007](#ref-mccune2007ImprovedEstimatesIncident))]. Both HLI and TPI3 were calculated in R using the spatialeco package ([Evans and Murphy, 2021](#ref-spatialEco)). We also included soil properties in our models of aspen habitat suitability. Specifically, we obtained 30-m probabilistic maps of soil pH, the percentage of organic material, the percentage of clay, and saturated soil water content from the POLARIS database ([Chaney et al., 2019](#ref-chaney2019POLARISSoilProperties)). We did not include elevation, latitude, and longitude as predictors in our modeling because we assumed these relationships were only correlative ([Araújo et al., 2019](#Xa394076d2f0f03ea6b9000cd6143e30f891c94f)). Instead we compare model residuals with these variables.

Table 1: Predictor variables selected for modeling the distribution of aspen

| Variable | Description | Expected relationship with aspen |
| --- | --- | --- |
| ADI | annual dryness index: (degree-days above 5 °C)^0.5 / (mean annual precipitation) | Fast-growing, short-lived species such as aspen typiclaly have high water demand (Ireland et al. 2014). Thus high ADI has been linked with lower climate suitability for aspen( Rehfeldt et al. 2009, 2015). |
| GSP | growing season (Apr - Sep) precipitation (mm) | Greater precipitaiton during the growing season may alleviate summer moisture stresss (Worral et al. 2013). |
| GSPDD5 | growing season precipitation to degree day ratio: (GSP/DD5) | Seasonal moisture stress may be lower in locations with greater growning season precipitaiton and shorter a growing season (i.e., high GSPDD5) may (Rehfeldt et al. 2009). |
| PRATIO | mean precipitation ratio: (growing season precipitation) / (mean annual precipitation) | Evenly distributed precipitation (intermediate PRATIO) may promote aspen by limiting seasonal moisture stress (Rehfeltd et al. 2009) |
| RH | mean annual relative humidity (%) | Higher relative humidity may limit seasonal moisture stress. |
| TD | difference between MCMT and MWMT (°C) | Identified as important predictor by Rehfeldt et al. (2015) and Worrall et al. (2013) |
| Clay | clay | High clay contents may inhibit aspen growth (Jones and DeByle 1985) |
| HLI | heat load index | Greater HLI may inhibit aspen, particularly at warmer sites |
| TPI3 | topographic position index calculated using a 3 x 3 cell neighborhood | Aspen is expected grow better in valley bottoms (low TPI) and on benches (moderate TPI) than steep slopes (high TPI) (Jones and DeByle 1985) |

### Data processing

## Modeling Approach

#### Overview

To characterize suitable habitat for aspen, we used four different modeling approaches commonly applied in species distribution modeling, generalized linear models (GLMs), generalized additive models (GAMS), and random forests (RFs), and regularized gradient boosted tree (RGBTs). Here, we first overview our modeling approach before describing specifics for individual modeling techniques. All models were fit in *R* ([R Core Team, 2022](#X4878592beea4a6dfca9c91383c925df652b2c7a)) using the *tidymodels* framework ([Kuhn and Wickham, 2020](#ref-tidymodels)).

To build GLM, GAM, RF, and GBT models, we first constructed a balanced data consisting of 10,000 pixels with aspen present and 10,000 pixels without aspen. To minimize the potential effects of spatial autocorrelation, pixels were selected so that they were separated by at least 1 km. To improve modeling fit and interpretability, all predictor variables were standardized by calculating the z-score. Using this dataset, we reduced our set of topoclimatic predictors to minimize the potential effects of collinearity on model inference and projection. Specifically, we used the *spatialRF* ([Wright and Ziegler, 2017](#ref-spatialRF)) to identify variables with a variable inflation factor greater than 5. When these conditions were met, variables were removed preferentially (Table 1.

To build and evaluate models, we then split our dataset into equally-sized testing and training datasets. The testing dataset was further split to create five spatial cross-validation folds using the *spatialsample* package ([Mahoney et al., 2023](#ref-spatialsample)). We then tuned model hyperparameters using spatial cross-validation and identified the best parameters based on the area under the receiver operator curve. To evaluate model performance in three ways, we used three approaches, but for each approah calculated the following statistics: XX.. First, we used spatial cross-validation to evaluate the capacity of our model to predict to new areas. Second, we evaluated performance on the testing dataset. Third, we compared the predictions with an independent data set of aspen presence. In all cases, we calculated

For each model we determined variable importance using a model-agnostic permutation-based approach, where each variable is randomized and then the ROC AUC statistic is compared with ROC AUC for the full model (where data has not been randomized). We evaluated the relationship between aspen presence and each predictor variable using accumulated local effects (ALE) profiles. Both variable importance and ALE were calculated in R using the DALEX package ([Biecek, 2018](#ref-DALEX)).

#### Generalized linear models

GLMs are extensions of parametric linear regression adapted to distributions other than the normal distribution. Here we used GLMs with a logit link function and a binomial error distribution to account for the structure of presence-absence data. We included both linear and quadratic effects for all variables, but did not explore any interaction terms. We fit the GLM using a Lasso regularization approach, which allows for model coefficients to be reduced to zero, thereby controlling for model complexity and improving tradeoffs between bias (i.e., the difference between the mean prediction from a model and the true value) and variance (i.e., the variability surrounding a prediciton) ([Hastie et al., 2009](#X1bac580b2d504864f7c67f41ed89ab717da9984)). Using spatial cross-validation, we tuned to the lasso penalty term prior to constructing the final model on the testing dataset. GLMs were fit using the *glmnet* package ([Friedman et al., 2010](#ref-glmnet)).

#### Generalized additive models

GAMS were fit using restricted maximum likelihood (REML), following recommendations from Pedersen et al.([2018](#X9ce84d2edd409eea4a5bb93b0b43ed50266fe99)). We set the k parameter, which sets t number of basis functions to the default value of 10.

#### Random Forests

RF models are an extension of classification and regression trees (CART), a nonparametric approach useful for modeling the nonlinear relationships and complex interactions that characterize ecological relationships ([Cutler et al., 2007](#X8af443e7151d3081ddf81ae6488f6e02a99b7ea)). In RF models, many trees are fit and combined using a bagging approach. Using spatial cross-validation, we tuned the number of variables to try at each split (mtry) and the minimum number of data points in a node that is required for the node to be split further (min\_n), while holding the number of trees constant at 1000. RF models were fit using the tidymodels implementation of the *ranger* package ([**ranger?**](#ref-ranger)).

#### Regularized gradient boosting trees

Gradient boosted trees (GBTs) are also an ensemble-based extension of CART. In contrast to RF approaches where trees are built in parallel, in gradient boosting approaches decision trees are constructed iteratively so that each successive tree attempt to improve upon predictions made by the previous tree. The iterative nature GBTs are prone overfitting, but this can be limited by including a learning rate parameter, which controls the rate at which the boosting algorithm adapts, and incorporating randomness into the tree construction by either sampling cases or variables for model building. RGBTs incorporate regularization terms that constrain the depth of the tree and gain in model fit required to further partition a node of the tree.

Here we used the xgboost implementation ([Chen et al., 2023](#ref-xgboost)). We used spatial cross-validation to tune min\_n, mtry, the maximum depth of the tree (tree\_depth), the loss reduction (loss\_reduction)

RGBTs were fit using the tidymodels implementation of the *xgboost* package [@xgboost], a fast and accurate implementation.

, , the reduction in the loss function required to split further (loss\_reduction), the learning rate (learn\_rate) and the maximum depth of the tree (tree\_depth), . RGBTs were fit using the package xgboost he XGBoost algorithm does parallelization within a single tree, th

#### Ensemble Model

We calculated a weighted probability of occurrence from all three presence-absence models. Weights assigned were based on the ROC AUC statistic.

## Projection

# Results

## Model performance

All models were accurate classifiers (Table 2). Nonparametric approaches were generally better than parametric approaches at predicting aspen presence (i.e., higher sensitivity), however parametric approaches were more balanced in their capacity to predict both aspen presence and absence. Based on AUC, the ensemble model outperformed each individual model. Further,

The ensemble model correctly predicted the presence of aspen for 71% of points identification points (n=12470).

Model results were spatially-biased. Across, all models the probability of aspen occurrence on the eastern slope of the Rocky Mountains

(Table 5).

Table 2: Model performance statistics. Observed values are from independent testing data.

| Model | Accuracy | F measure | kappa | Precision | Recall | AUC | Sensitivity | Specificity |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Ensemble | 0.77 | 0.77 | 0.53 | 0.76 | 0.78 | 0.84 | 0.78 | 0.76 |
| GAM | 0.75 | 0.75 | 0.50 | 0.75 | 0.74 | 0.83 | 0.74 | 0.76 |
| GLM | 0.74 | 0.73 | 0.48 | 0.76 | 0.70 | 0.81 | 0.70 | 0.77 |
| RF | 0.72 | 0.75 | 0.45 | 0.69 | 0.81 | 0.81 | 0.81 | 0.64 |
| XGB | 0.73 | 0.75 | 0.46 | 0.69 | 0.82 | 0.82 | 0.82 | 0.64 |

### Variable importance

(Fig. 2.

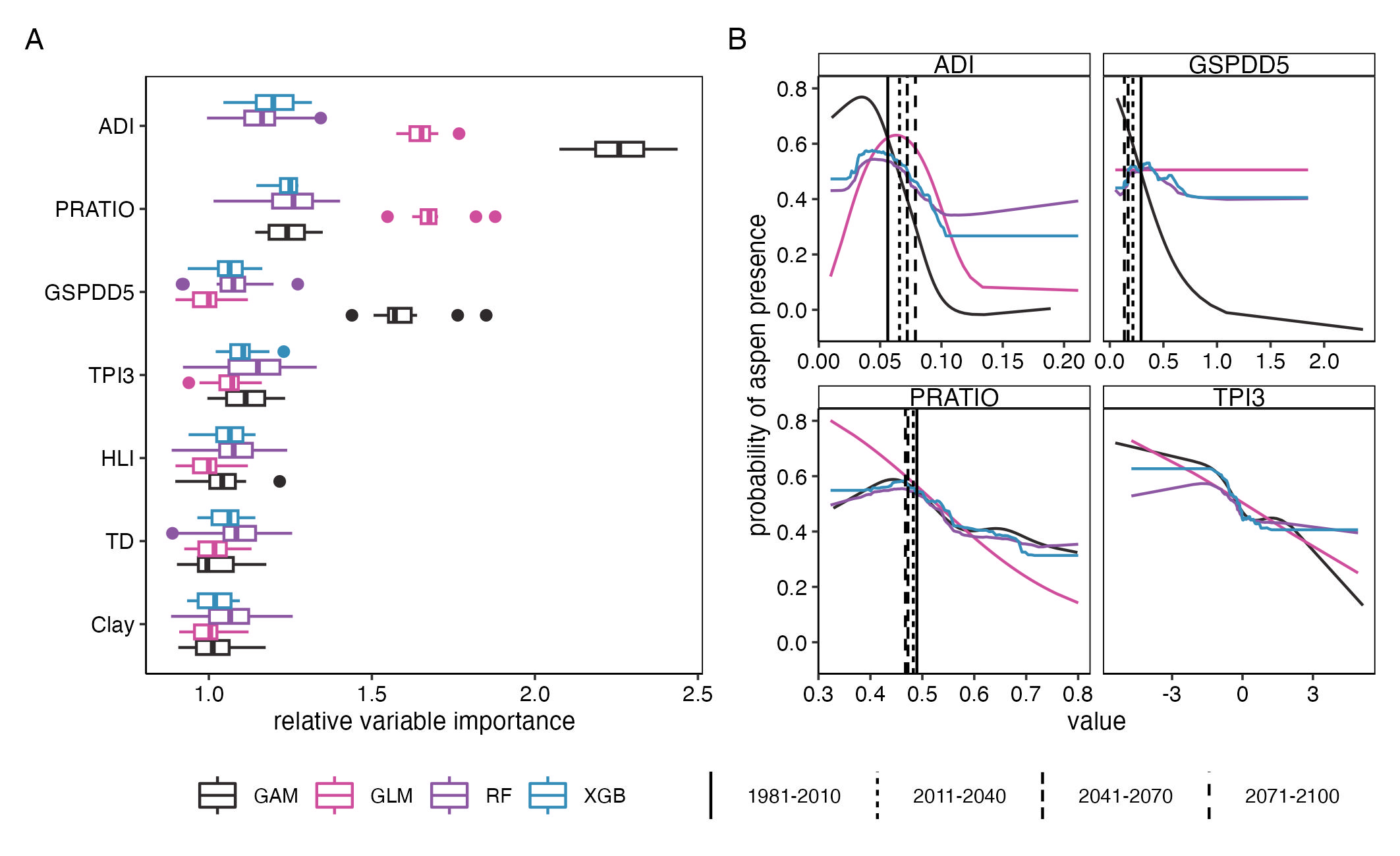


Figure 2: Variable importance scores (A) and accumulate local effects (B) for models of aspen habitat suitability by modeling approach. In B, vertical lines illustrate the mean climate conditions for areas with existing aspen for the historical period (1981-2010) and projections for the 2011-2040, 2041-2070, and 2071-2100 periods under the SPP4-8.5 scenario. For variable definitions and descriptions see Table 1.

(Fig. 3.

(Fig. 4.

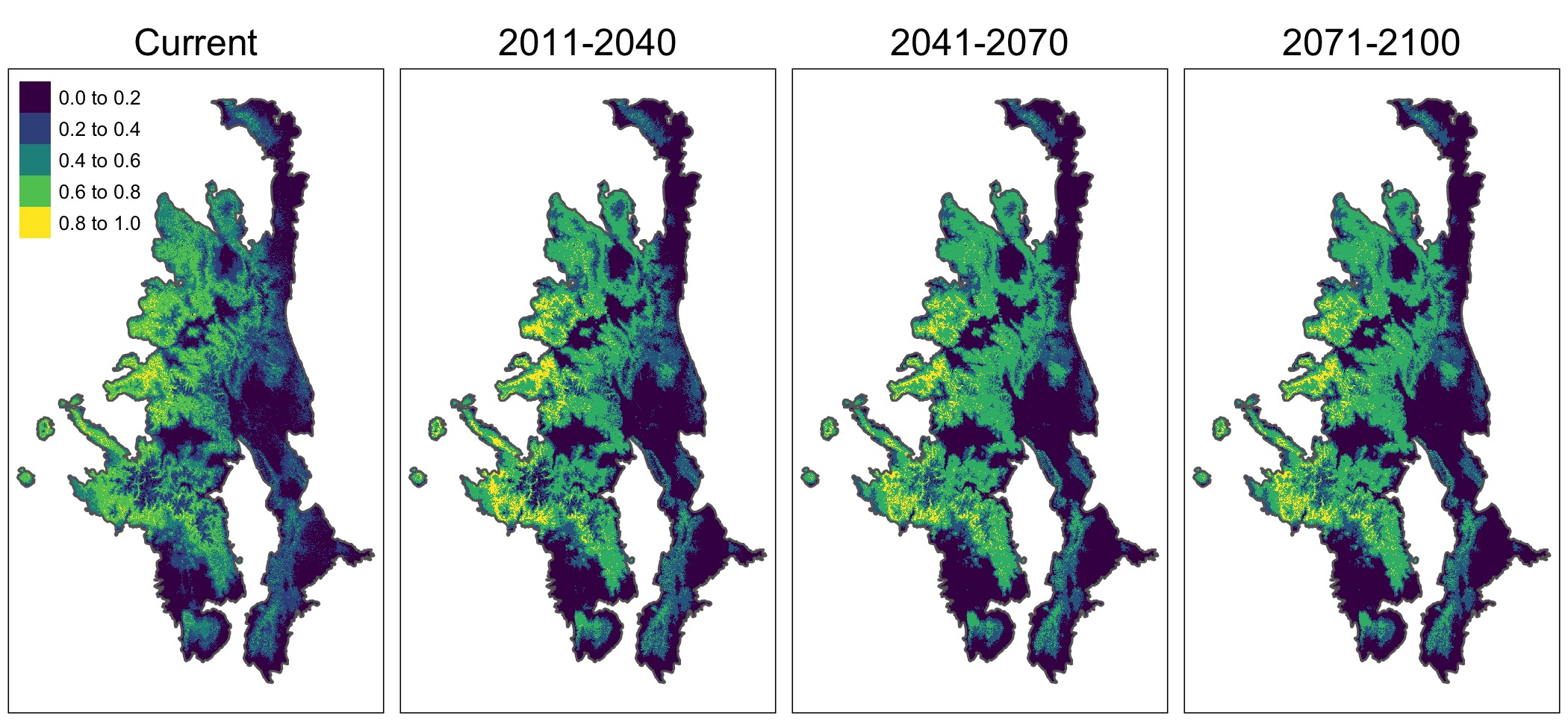


Figure 3: The ensemble projection of aspen habitat suitability under current conditions and projections for future periods based on an SSP5-8.5 scenario.

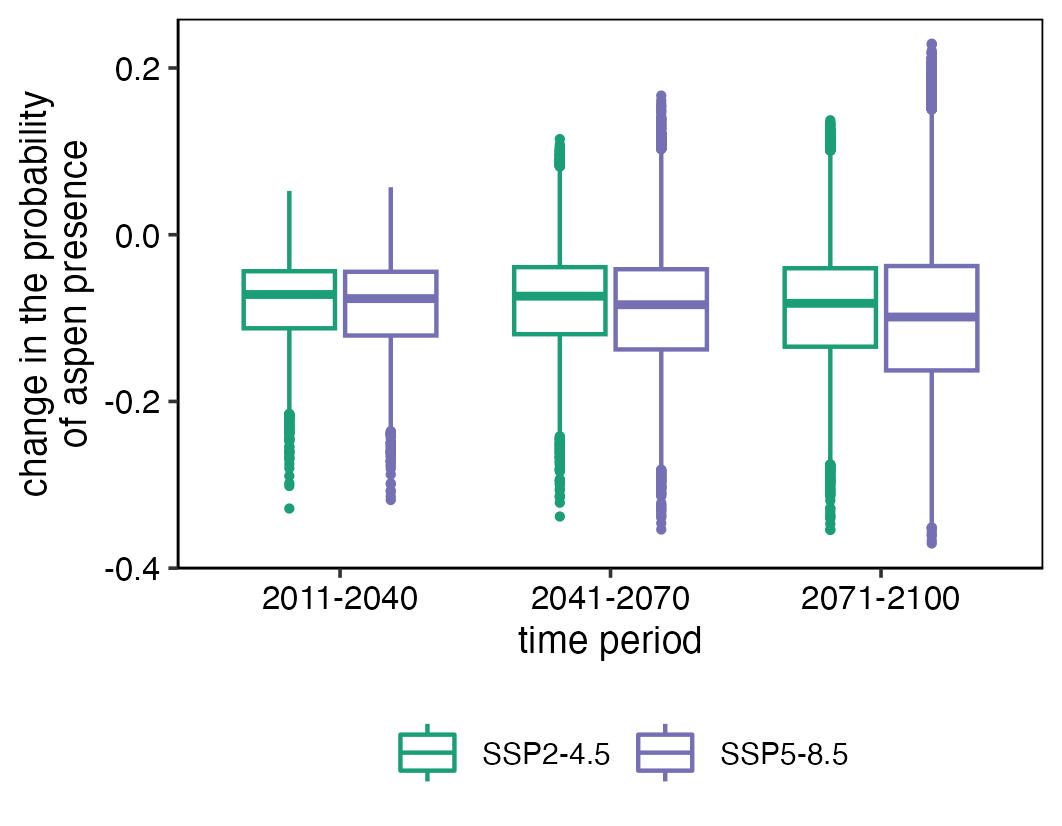


Figure 4: Change

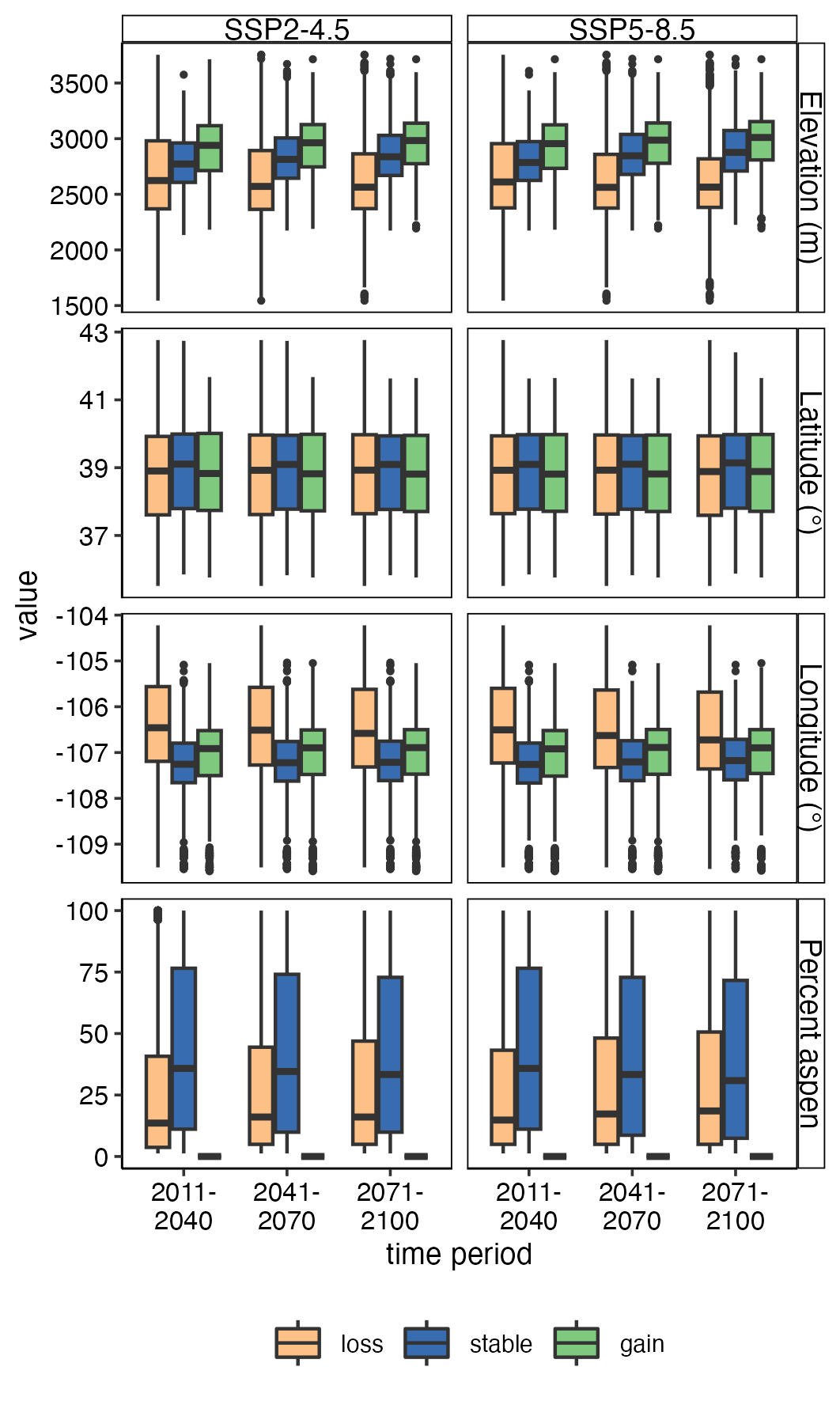


Figure 5: GainLoss-Geo

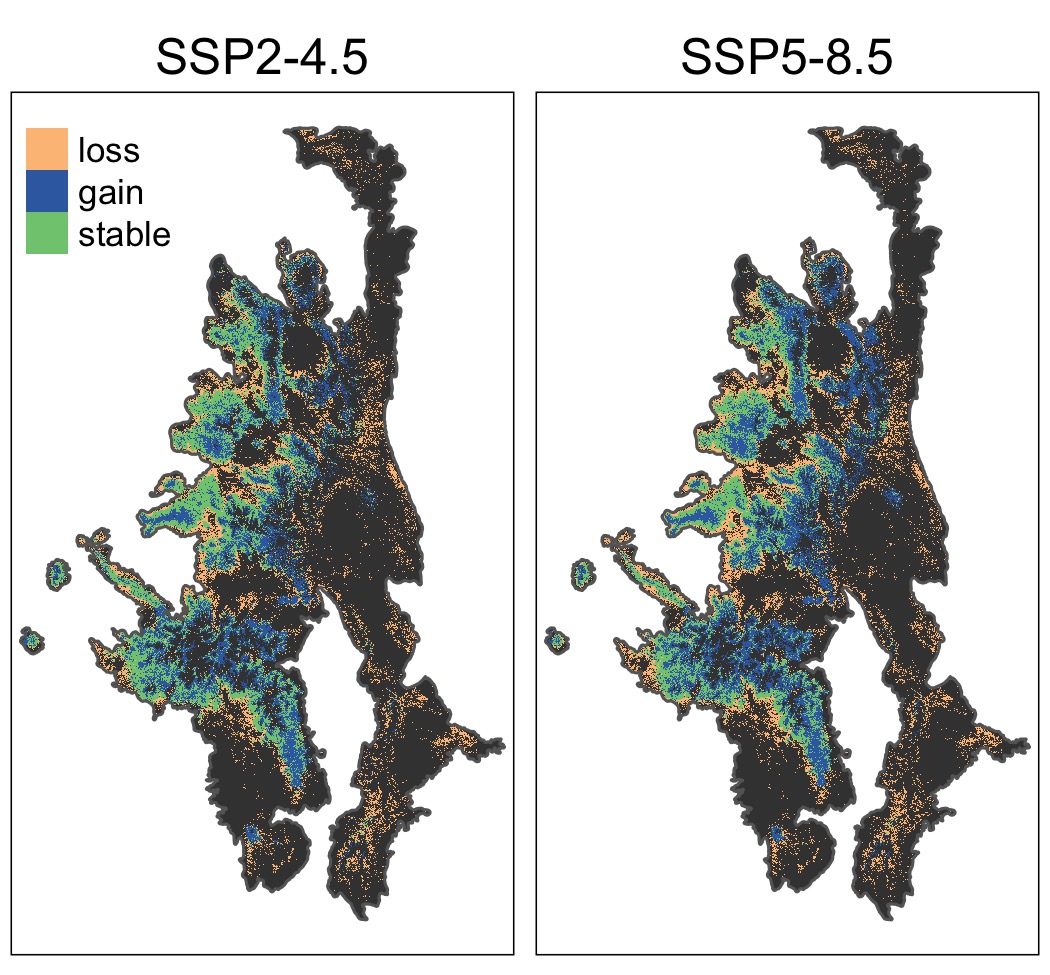


Figure 6: LossGainMaps

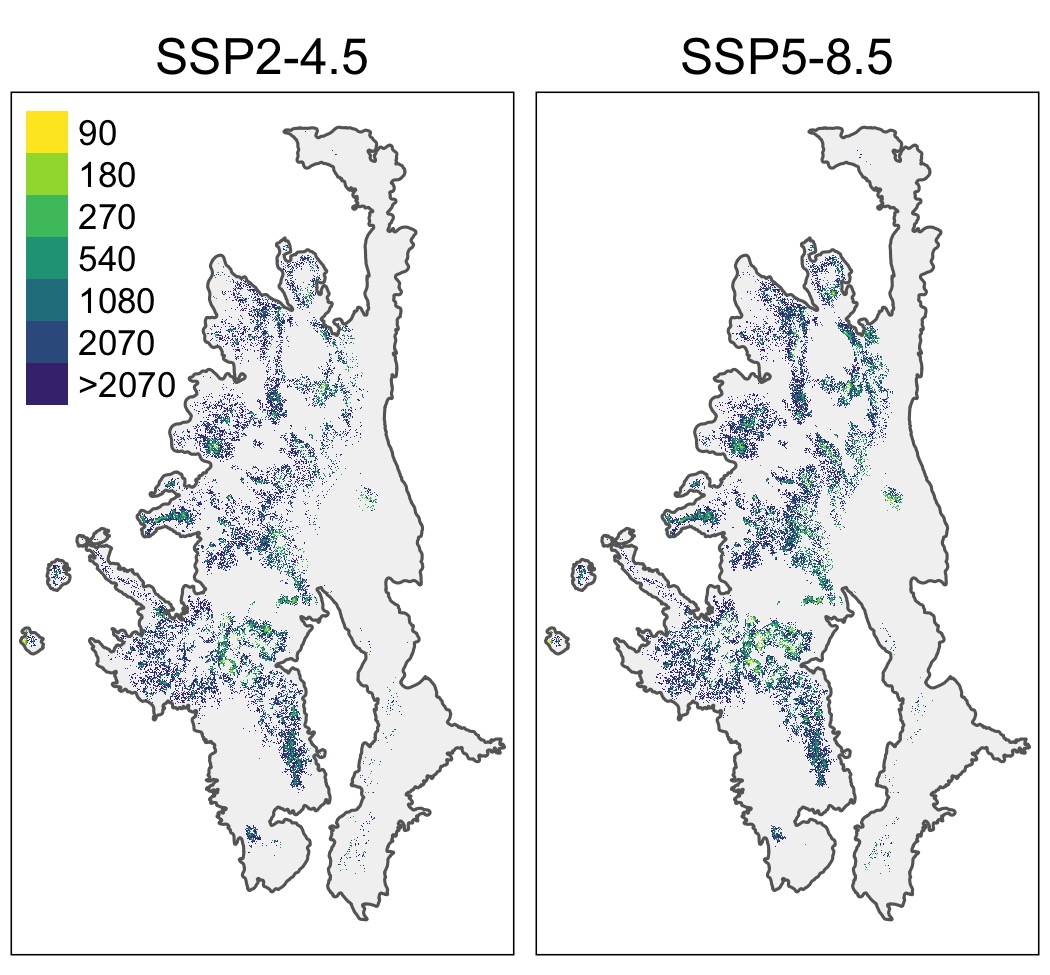


Figure 7: GainDistanceMaps

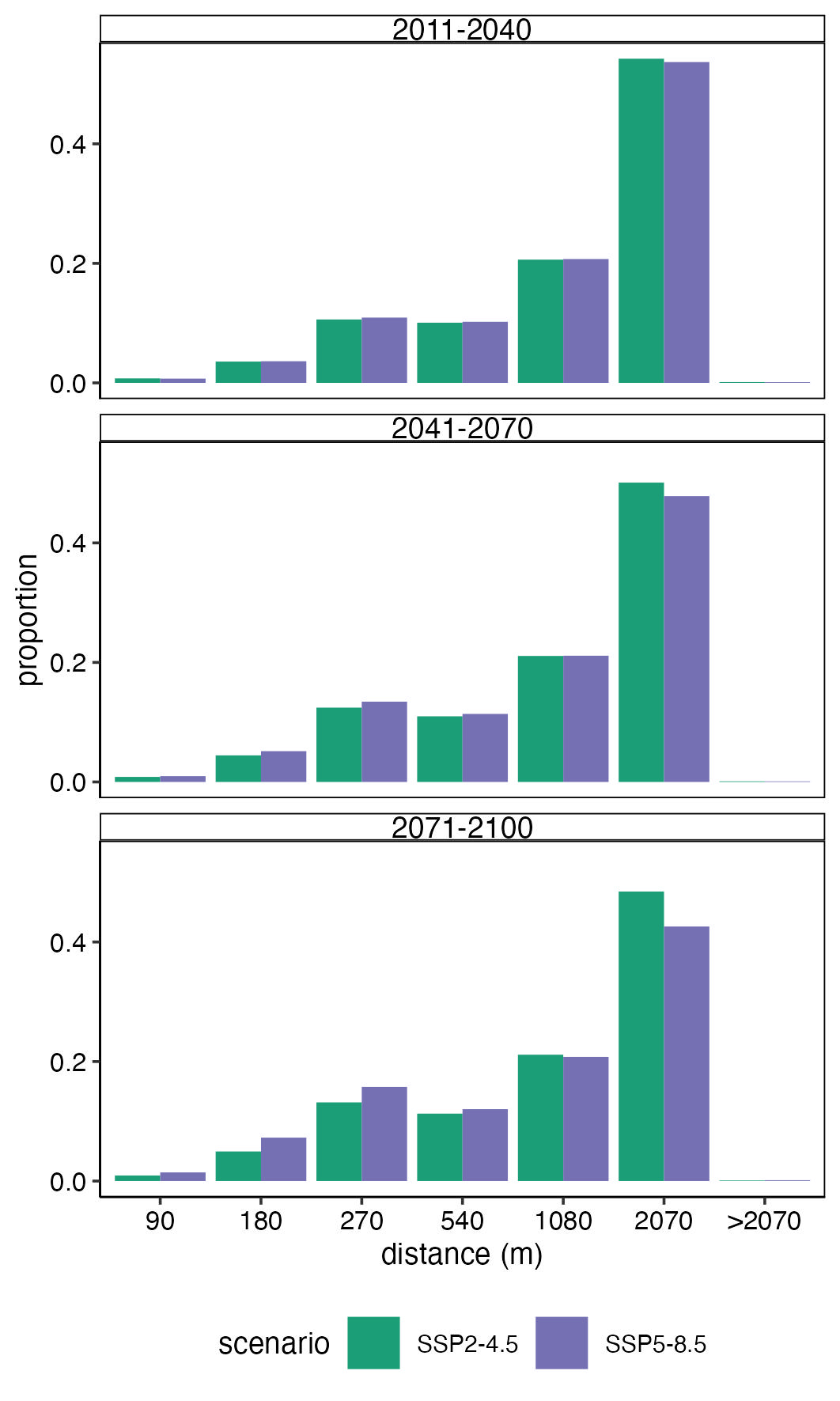


Figure 8: GainDistanceMaps

# Discussion

Quaking aspen is one of the most widely distributed tree species. While our study area clearly includes areas where aspen is absent, we acknowledge that our dataset may be environmentally truncated ([Hannemann et al., 2016](#ref-hannemann2016DevilDetailUnstable); [Thuiller et al., 2004](#Xb5e3a842768cfe7ba494facd83499a616e17792)).

# Conclusions

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# Appendix A: ODMAP

## Overview

Here we describe the SDMs produced herein following the Overview, Data, Model, Assessment, Prediction (ODMAP) protocol for species distribution models ([Zurell et al., 2020](#ref-zurell2020StandardProtocolReporting)). Here, we first provide the Overview for our modeling, while the remaining ODMAP sections are detailed in Table S3.

The objectives of this modelling exercise are to (1) better explain the drivers of aspen’s distribution across the Southern Rocky Mountains, (2) map the area suitable for aspen, and (3) forecast the area suitable for aspen presence in the future under two different climate scenarios.

Table 3: ODMAP protocol information. Details on Data, Model, Assessment, Prediction. For Overview section, please refer to main text.

| ODMAP element | Contents |
| --- | --- |
| Overview |  |
| Authorship | Authors: Sarah J. Hart, Asha Paudel, Maxwell Cook |
|  | Contact email: sarah.hart@colostate.edu |
|  | Title: |
|  | DOI: |
| Model objective | Objective: Inference, Mapping, and Forecasting |
|  | Target outputs: continuous occurrence probabilities, binary maps of potential presence, and maps of potential loss, gain, and stable habitat |
| Taxon | Quaking aspen (Populus tremuloides) |
| Location | Southern Rocky Mountains, US |
| Scale of analysis | Spatial extent (Lon/Lat): Longitude 103.86 ° W - 109.61 ° W, Latitude 35.28 ° N - 47.78 ° N |
|  | Spatial resolution: 90 x 90 m |
|  | Temporal resolution and extent: We modelled the presence of aspen based on remotely sensed maps generated from imagery collected in XXXX |
|  | Type of extent boundary: ecoregion (Southern Rocky Mountains) |
| Biodiversity data overview | Observation type: remotely sensed |
|  | Response type: presence/absence |
| Type of predictors | Climatic, topographic, edaphic |
| Conceptual model / Hypotheses | Based on previous studies, we tested climate, topography and edaphic factors as important environmental predictor variables for aspen presence in the Southern Rocky Mountains. |
| Assumptions | We make the following key assumptions:  (1) aspen is at pseudo-equilibrium with the environment  (2) topography, climate, and soil conditions are the key drivers of aspen's distribution  (3) classification error (estimated at XX) in maps of aspen occurrence were negligible  (4) the relationship fit under current conditions apply to future climate conditions (i.e., no change in key limiting processes) |
| SDM algorithms | Algorithms: SDMs were fit using four different algorithms: generalized linear models (GLMs), generalized additive models (GAMs), gradient boosted trees (GBTs), and random forests (RFs). |
|  | Model complexity: We chose different modelling parameters to optimize each statistical technique. |
|  | Ensembles: We combined the four SDMs to generate an ensemble prediction |
| Model workflow | Prior to model building, all predictor variables were standardized. Model hyperparemeters were then tuned using a spatial cross-validation approach, with the best parameters selected using the area under the reciever operating chracteristic (ROC) curve (AUC). |
| Software | Software: All analyses were conducted using R version 4.3.1 (R Core Team 2023) with the packages XXX, XXX, XXX |
|  | Code availability: All code is publicly available on GitHub (LINK) |
|  | Data availability: Data are available from XXXX |
| Data |  |
| Biodiversity data | Taxon names: Trembling aspen (Populus tremuloides) |
|  | Taxonomic reference system: US Department of Agriculture (USDA) Plant List of Attributes, Names, Taxonomy, and Symbols (PLANTS) Database |
|  | Ecological level: population |
|  | Data source: Aspen presence-absence data at 10x10 m spatial resolution were obtained from Cook et al. (XXXX) |
|  | Sampling design: |
|  | Sample size: The aspen dataset consists of 4,312,302,640 10 x 10 m cells, of which 117,140,964 recorded the presence of aspen. |
|  | Ecoregion mask: We clipped all data to the Southern Rocky Mountain Ecoregion using data from the EPA's (2013) Level III Ecoregions of the Conterminous United States product. |
|  | Scaling: We aggregated the aspen presence-absence data to a 90 x 90 m cell size. |
|  | Data filtering: |
|  | Absence data: The Cook et al. (XXXX) map consists of both presence and absence data. |
| Data partitioning | To reduce computation time, we randomly selected 10,000 cells for model building and 10,000 cells model testing. To reduce the potential effects of spatial autocorrelation, all sample points were separated by a distance of at least 1 km. |
| Environmental data/predictor varaibles | Predictor variables:  (1) Topography: topographic position index, heat load index (HLI)  (2) Climate: 35 climate variables (see Table XX)  (3) Soils: percent clay, percent soil organic matter, saturated water content |
|  | Data sources:  (1) Topography: 3DEP DEM (USGS XXX).  (2) Climate: AdaptWest Project (2022)  (3) Soils: POLARIS soil properties database (Cheney et al. 2019). |
|  | Spatial resolution and extent of raw data: All data were available for the entire study area.  (1) Topography: The raw resolution of the topographic data was 30 m.  (2) Climate: The raw resolution of the topographic data was 1 km.  (3) Soils: The raw resolution of the topographic data was 30 m. |
|  | Temporal resolution and extent of raw data:  (1) Topography: raw topographic data were collected over the period 2009-2023  (2) Climate: mean monthly climate data the period 1981-2010  (3) Soils: integrate data collected over the 1899 to 2019 period as part of the National Cooperative Soil Survey |
|  | Geographic projection of raw data:  (1) Topography: NAD83(HARN) / Conus Albers (EPSG:5071)  (2) Climate: Lambert Azimuthal Equal Area (EPSG:9820)  (3) Soils: WGS 84 (EPSG:4326) |
|  | Data processing: (1) Topography: We cacluated the Heat Load Index (HLI) and topographic position index (TPI) using the spatialeco package (REF). TPI was calculated using a 3 cell neighborhood (i.e. 90 x 90 m) and a 15 cell neighborhood (i.e. 450 x 450 m). TPI and HLI datasets were then aggregated to 90 m using the mean value and reprojected to Universal Transmercator (UTM) Zone 13N.  (2) Climate: We calculated ADI, GSP, PRATIO, and GSPDD5 following Rehfeldt et al. (2009). All climate varaibles were then downscaled to 250 m resolution using gradient and inverse distance squared (GIDS) interpolation.  (3) Soils: Soil data were aggregated to 90 m using the mean value and reprojected to Universal Transmercator (UTM) Zone 13N. |
| Model |  |
| Variable pre-selection | We initially reduced our set of climate predictor variables by first calcuating pairiwise Spearman's correlations and then fitting univriate random forest models of the presence/absenece using raw climate data (i.e., 1 km resoltuion not the 250 m downscaled product). When |r|>0.75, we retained the variable with greatest contribution to AUC, calcuated from the univariate model. |
| Multicollinearity | Using the downscaled climate varibles, we reduced multicollinearity in our predictor dataset by calculating variable inflation factors (VIF). When VIF >5, variables were iteratively removed, giving preference to climate variables (ordered by contribution to AUC from the univariate RF model) using the spatialRF package (Benito 2022). |
| Model settings | (1) The GLM was fit using a logit link function and a binomial error distribution. For all variables, we included both linear and quadratic effects. Models were fit using a Lasso regularization approach. The only tuned the penalty factor. Based on the higest AUC, the penalty factor was set to XX. We did not explore any interaction terms.  (2) The GAM was was fit using a logit link function and a binomial error distribution. For all variables, we used thin plate regression splines as the smooth basis and set bias demensions term (k) to the default value of 10. To prevent overfitted, we allowed We tuned the moothness adjust Models were fit using restricted maximum likelihood (REML). We did not explore any interaction terms.  (3) For the RF model, we tuned the minimum number of data points in a node that is required for the node to be split further (min\_n) and the number of variables to try at each split (mtry). Based on highest AUC, min\_n = XXX an//d mtry = XXX.  (3) GBT: For the GBT model, we tuned the minimum number of data points in a node that is required for the node to be split further (min\_n), the reduction in the loss function required to split further (loss\_reduction), the learning rate (learn\_rate) and the maximum depth of the tree (tree\_depth). Based on highest AUC, min\_n = XXX, loss\_reduction = XXX , learn\_rate = XXX , and tree\_depth = XXX. |
| Model estimates | Using the R package DALEX (REF), we determined variable importance using a model-angostic permutation-based approach. In this approach, each variable is randomized and then the ROC AUC statistic is compared with ROC AUC for the full model (where data has not been randomized). We evaluated the relationship between aspen presene and each predictor variabele using accumulated local effects (ALE) profiles, which were generated using the ingrediates package (REF). |
| Model averaging / Ensembles | We calculated a weighted probabilty of occurrence from all three presence-absence models. Weights assigned were based on the ROC AUC statistic. |
| Non-independence | We evaulated the potenital effects of spatial autocorrelation on our models' predictive ability using a spatially clustered cross-validation approach. |
| Threshold selection | Binary predictions were derived by maximizing Youden's J statistic, which balances sensitivity and specificty (Youden 1950). |
| Assessment |  |
| Performance statistics | Predictive model performancWe on validation data was assessed using X different performance measures: area under the reciever opperator curve (AUC), sensitivity, specificity, overall accuracy, kappa, F measure, Precision, and Recall |
| Plausibility checks | We checked model plausibility by assessing accumulated local effects plots. |
| Prediction |  |
| Prediction output | For further analyses, we used continuous predictions of occurrence probability, as well as predicted presence-absence, which was obtained by binarising the predicted occurrence probabilities using the TSS-maximization threshold. |
| Uncertainty quantification | We account for algorithmic uncertainty by applying an ensemble approach averaging over three different SDM algorithms. |

# Appendix B: Collinearity

Table 4: Climate variables considered for inclusion in SDMs and modeling notes.

| Group | Variable | Description | Findings from previous research | Variable importance | Preference order | Modeling notes |
| --- | --- | --- | --- | --- | --- | --- |
| Temperature-precip | ADI | annual dryness index: (DD5^0.5)/MAP | Identified as important predictor by Rehfeldt et al. (2009) and (2015). | 0.48 | 1 | retain |
| Seasonality | bFFP | Julian date on which the frost free period beings |  | 0.20 | 28 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature-precip | CMD | Hargreaves climatic moisture deficit (mm) |  | 0.30 | 17 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature-precip | CMI | Hogg’s climate moisture index (mm) |  | 0.45 | 11 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Seasonality | DD\_0 | degree-days below 0 °C |  | 0.31 | 15 | retain |
| Seasonality | DD\_18 | degree-days below 18 °C |  | 0.40 | 12 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Seasonality | DD1040 | degrees-days above 10 °C and below 40 °C |  | 0.31 | 16 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Seasonality | DD18 | degree-days above 18 °C |  | 0.23 | 21 | removed - initial screening showed strong correlation (r≥0.75) with DD\_0 |
| Seasonality | DD5 | degree-days above 5 °C | Identified as important predictor by Worrall et al. (2013) and Greer et al. (2016). | 0.36 | 3 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Seasonality | eFFP | Julian date on which the frost free period ends |  | 0.16 | 33 | removed - initial screening showed strong correlation (r≥0.75) with DD\_0 |
| Temperature | EMT | extreme minimum temperature (°C) |  | 0.21 | 26 | removed - initial screening showed strong correlation (r≥0.75) with DD\_0 |
| Temperature-precip | Eref | Hargreave's reference evapotranspiration (mm) |  | 0.28 | 18 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature | EXT | extreme maximum temperature (°C) |  | 0.20 | 30 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Seasonality | FFP | mean annual length of the frost-free period (days) |  | 0.19 | 31 | removed - initial screening showed strong correlation (r≥0.75) with DD\_0 |
| Precipitation | GSP | growing season (Apr - Sep) precipitation (mm) | Idenified as important predictor by Worrall et al. (2013) | 0.23 | 8 | retain |
| Temperature-precip | GSPDD5 | growing season precipitation to degree day ratio: (GSP/DD5) | Identified as important predictor by Rehfeldt et al. (2009). | 0.46 | 5 | retain |
| Precipitation | MAP | mean annual precipitation (mm) | Identified as important predictor by Worrall et al. (2013). | 0.35 | 6 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature | MAT | mean annual temperature |  | 0.23 | 22 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature | MCMT | mean coldest month temperature (°C) |  | 0.24 | 20 | removed - initial screening showed strong correlation (r≥0.75) with DD\_0 |
| Temperature | MWMT | mean warmest month temperature (°C) | Identified as important predictor by Rehfeldt et al. (2015). | 0.20 | 9 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Seasonality | NFFD | mean annual number of frost free days |  | 0.20 | 29 | removed - initial screening showed strong correlation (r≥0.75) with DD\_0 |
| Precipitation | PAS | mean precipitation as snow (mm) between August in previous year and July in current year |  | 0.35 | 13 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Precipitation | PPT\_at | mean autumn precipitation (mm) |  | 0.34 | 14 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Precipitation | PPT\_sm | mean summer precipitation (mm) |  | 0.17 | 32 | removed - initial screening showed strong correlation (r≥0.75) with TD |
| Precipitation | PPT\_sp | mean spring precipitation (mm) |  | 0.28 | 19 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Precipitation | PPT\_wt | mean winter precipitation (mm) | Idenified as important predictor by Worrall et al. (2013) | 0.32 | 7 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Precipitation | PRATIO | mean precipitation ratio:  GSP/MAP | Identified as important predictor by Rehfeldt et al. (2009). | 0.46 | 2 | retain |
| Temperature-precip | RH | mean annual relative humidity (%) |  | 0.09 | 34 | retain |
| Temperature | Tave\_at | mean autumn temperature (°C) |  | 0.21 | 27 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature | Tave\_sm | mean summer temperature (°C) |  | 0.22 | 24 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature | Tave\_sp | mean spring temperature (°C) |  | 0.22 | 25 | removed - initial screening showed strong correlation (r≥0.75) with ADI |
| Temperature | Tave\_wt | mean winter temperature (°C) |  | 0.23 | 23 | removed - initial screening showed strong correlation (r≥0.75) with DD\_0 |
| Seasonality | TD | difference between MCMT and MWMT (°C) | Identified as important predictor by Rehfeldt et al. (2015) and Worrall et al. (2013) | 0.18 | 10 | retain |
| Temperature | TMAX | Mean maximum temperature in warmest month | Identified as important predictor by Rehfeldt et al. (2009), Worrall et al. (2013), and Greer et al. (2016). | 0.21 | 4 | removed - initial screening showed strong correlation (r≥0.75) with ADI |

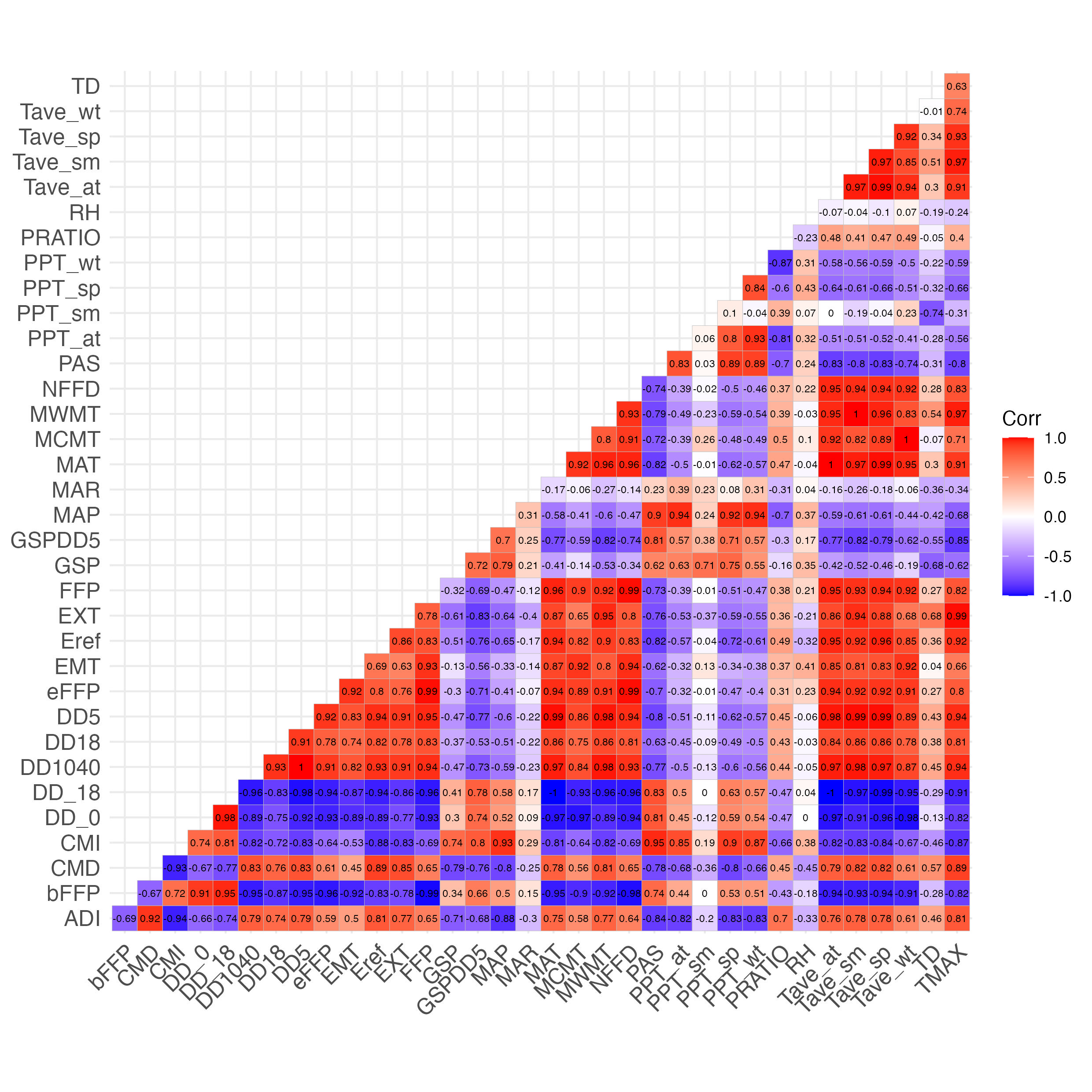


Figure 9: Spearman’s correlation coefficients between pairs of climate predictor variables

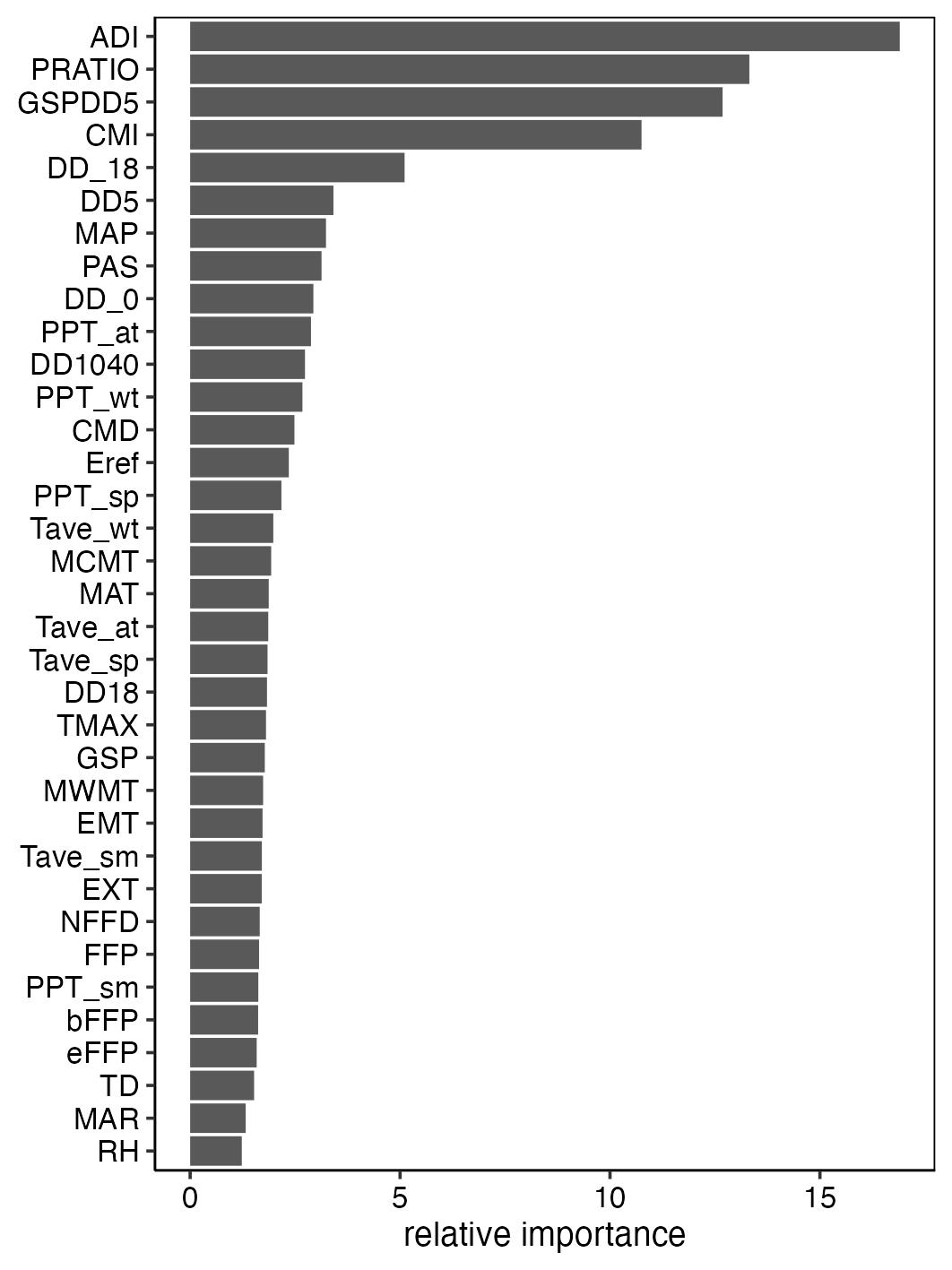


Figure 10: Contribution of climate predictor variables to univariate random forests models

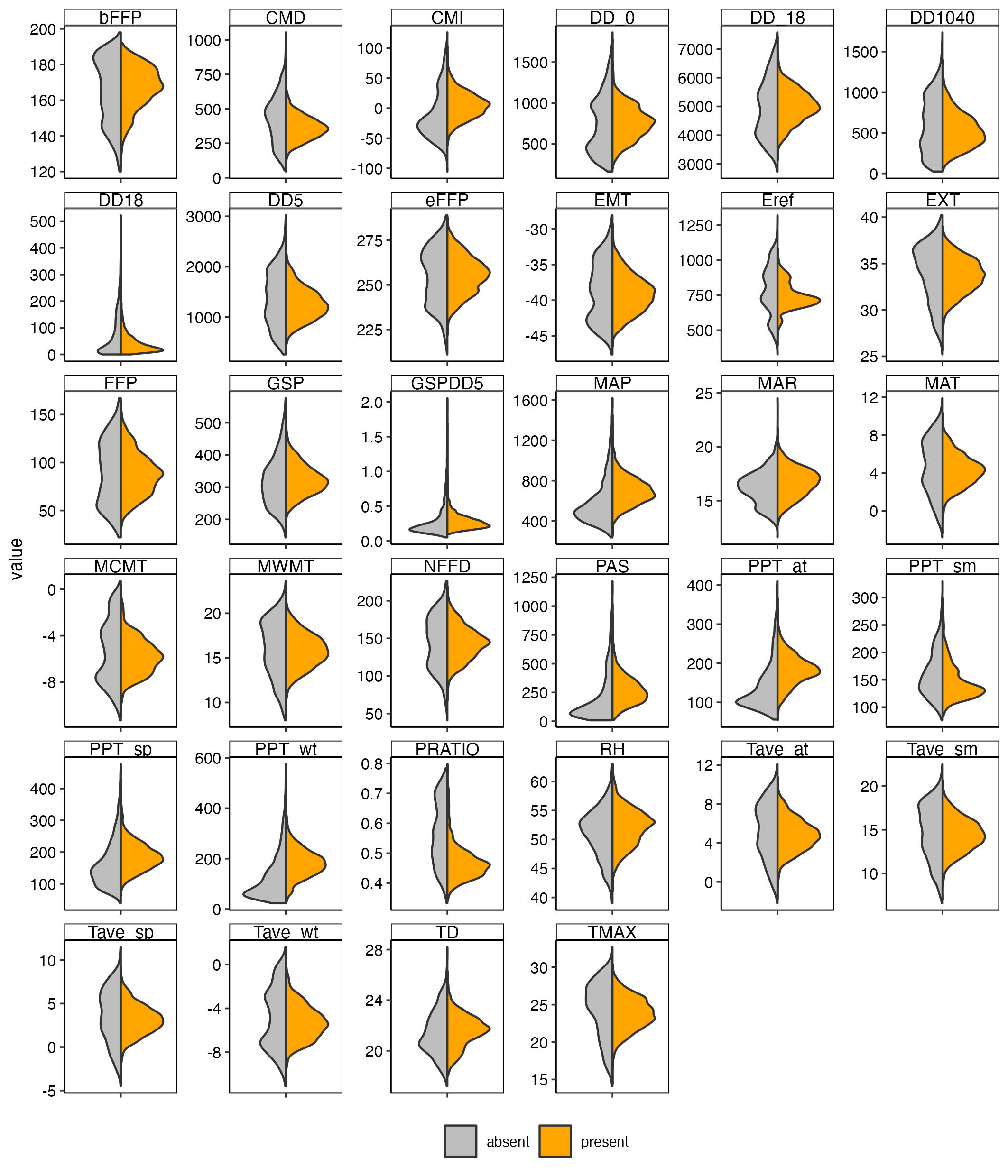


Figure 11: Paired violin plots illustrating the

# Appendix C: Model Performance

Table 5: Model performance statistics from spatial cross-validation. Values show the mean ± one standard error.

| Model | Accuracy | F measure | kappa | Precision | Recall | AUC ROC | Sensitivity | Specificity |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| GLM | 0.72 ± 0.02 | 0.71 ± 0.05 | 0.38 ± 0.05 | 0.77 ± 0.03 | 0.66 ± 0.07 | 0.78 ± 0.02 | 0.66 ± 0.07 | 0.73 ± 0.08 |
| RF | 0.77 ± 0.02 | 0.78 ± 0.04 | 0.46 ± 0.03 | 0.76 ± 0.03 | 0.8 ± 0.05 | 0.83 ± 0.01 | 0.8 ± 0.05 | 0.64 ± 0.08 |
| GBT | 0.77 ± 0.02 | 0.77 ± 0.04 | 0.44 ± 0.04 | 0.77 ± 0.02 | 0.77 ± 0.06 | 0.83 ± 0.01 | 0.77 ± 0.06 | 0.64 ± 0.1 |

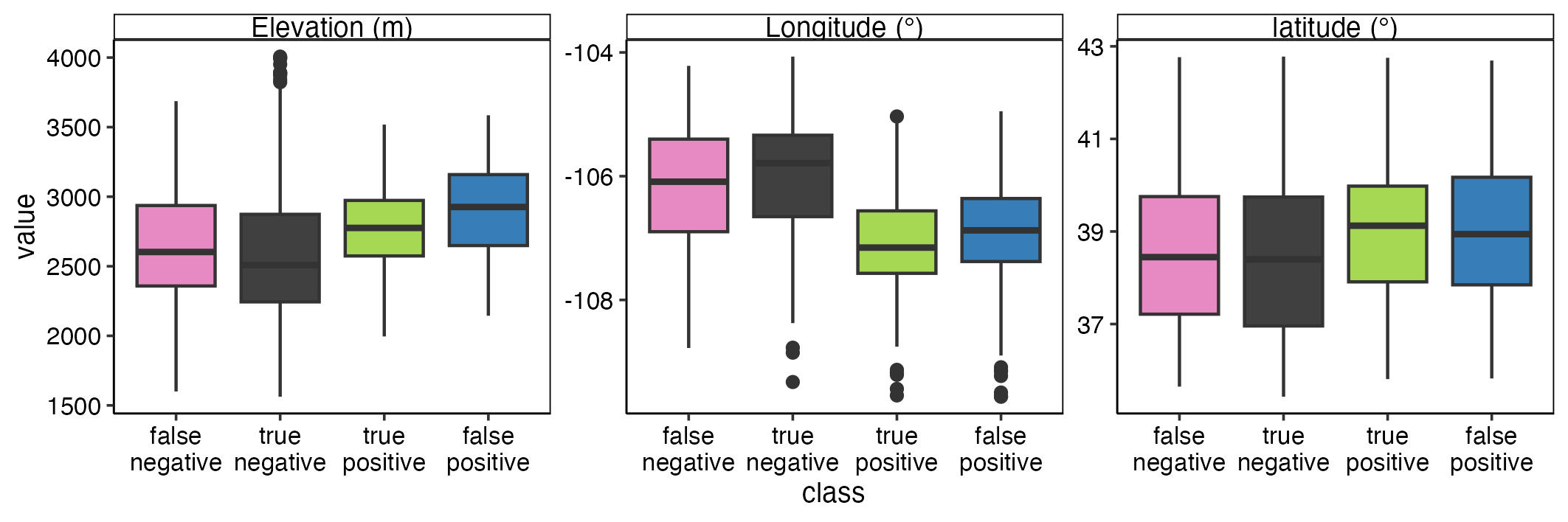


Figure 12: The relationship between geographic position and model performance.

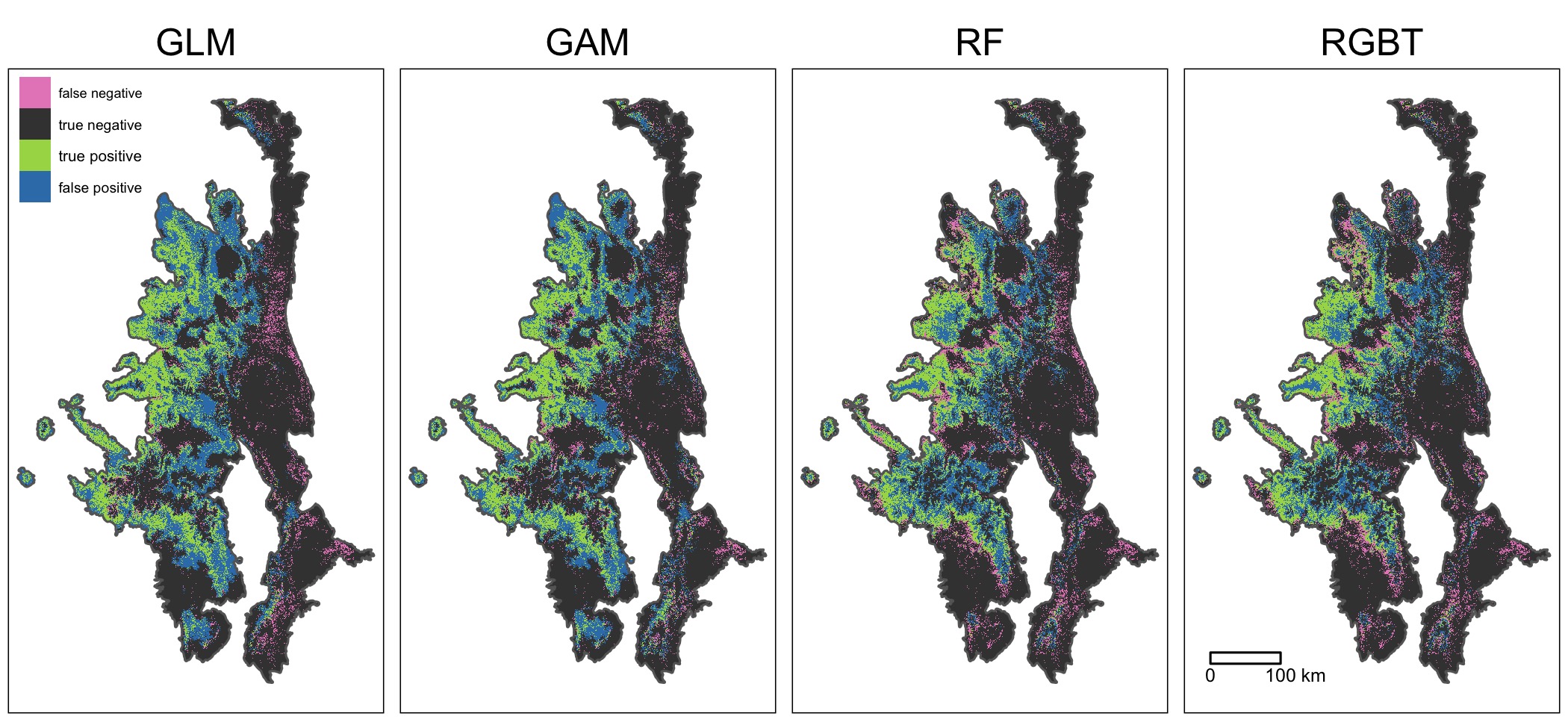


Figure 13: The relationship between geographic position and model performance.

# Appendix D