Wetlands (2016) 36:111–120
DOI 10.1007/s13157-015-0721-8

ORIGINAL RESEARCH

Developing a Field-Tested Wetland Indicator Rating for Blue Spruce (*Picea Pungens*) in the Southern Rocky Mountains

Edward A. Gage[1] **· David J. Cooper**[1] **· Betsy Bultema**[1] **· Cristina McKernan**[1] **· Robert Lichvar**[2]

Received: 7 April 2015 / Accepted: 12 November 2015 / Published online: 23 November 2015

Abstract To be identified as a wetland under U.S. Federal regulations, a site must, under normal circumstances, support vegetation dominated by hydrophytes. A list of hydrophytes and their wetland indicator rating is published by the U.S. Army Corps of Engineers as the National Wetland Plant List (NWPL) and is the basis for assessing the vegetation criteria of Federal wetland delineation manuals. Ratings are primarily based on expert opinion and few empirical studies have been done, particularly at landscape scales. In this study, we developed an approach for quantifying plant indicator ratings at broad spatial scales and used it to estimate the frequency that *Picea pungens* Engelm. (Colorado blue spruce) occurs in wetlands across a 22,921 km^2 study area in the southern Rocky Mountains. Species distribution models were developed and used to inform a multistage field sampling design. Wetland soil and hydrology indicators were assessed around 423 randomly selected trees in 22 HUC12 watersheds. Only 16.5 % of trees occurred in wetlands, suggesting that a rating of facultative upland (FACU) is more appropriate than the currently published rating of facultative (FAC) for our study area. This study demonstrates that it is feasible to quantitatively evaluate ratings for species even at broad landscape scales.

Electronic supplementary material The online version of this article (doi:10.1007/s13157-015-0721-8) contains supplementary material, which is available to authorized users.

✉ Edward A. Gage
edward.gage@colostate.edu

[1] Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA

[2] U.S. Army Corps of Engineers, Cold Regions Research and Engineering Laboratory (CRREL), Hanover, NH 03755, USA

Keywords Wetland delineation · Hydrophyte · National Wetland Plant List · Regulation · *Picea pungens*

Introduction

The identification and delineation of wetlands in the U.S. using U.S. Army Corps of Engineers (USACE) methods relies on the concept of wetland indicators – characteristics of soil, vegetation, and hydrologic regime that indicate the occurrence of wetland conditions (Tiner 1999; Environmental Laboratory 1987). To be classified as a wetland according to the USACE wetland delineation manual, a site must support hydric soils and a wetland hydrologic regime. In addition, under normal circumstances a site must also support vegetation dominated by hydrophytes, defined as "any macrophyte that grows in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content; plants typically found in wet habitats" (Environmental Laboratory 1987; Tiner 2012). Lists of hydrophytes were originally developed by National Wetland Inventory staff, panels of regional experts, and agency personnel and were published as the National List of Plant Species that Occur in Wetlands (Reed 1988; Tiner 2006). These lists are now administered by the USACE and updated as the National Wetland Plant List (NWPL; http://rsgisias.crrel.usace.army.mil/NWPL/) (Lichvar et al. 2014; Lichvar 2013).

Indicator ratings on the NWPL are a probabilistic assessment of the frequency that individuals of a species occur in wetlands and are assigned separately within each of the 10 USACE regions of the U.S. in which each species occurs. One of five indicator classes is assigned: obligate wetland species (OBL) almost always occur in wetlands (estimated probability >99 %), facultative wetland (FACW) species usually occur in wetlands (67–99 % probability), facultative

(FAC) species are equally likely to occur in wetlands or non-wetlands (34–66 %), facultative upland (FACU) species usually occur in non-wetlands (1–33 %) and obligate upland (UPL) species rarely occur in wetlands (<1 %) (Lichvar and Minkin 2008). Additions and revisions to the NWPL ratings are made by technical committees from each of the Corps wetland regions and are a collaborative effort with participation by four Federal agencies: Corps of Engineers, Environmental Protection Agency, Fish and Wildlife Service, and Natural Resources Conservation Service. The opinions of experts in botany and plant ecology are also solicited from government agencies, universities, and the private sector.

The indicator rating of each taxon is a non-quantitative assessment made by panel members using their experience, as well as floristic manuals, regional experts, and pertinent ecological literature, when it exists. However, most species ratings are untested hypotheses, and methods for analyzing the wetland indicator rating of a species have not been previously developed. Despite their importance to the outcome of wetland delineations, to our knowledge, the indicator rating of a species on the NWPL has never been explicitly and rigorously tested at a landscape or ecoregional scale. Such methods are essential for improving the rigor and overall accuracy of the NWPL.

Our objectives in this study were to (1) develop a general framework for quantifying the frequency that a plant occurs in wetlands (sensu the USACE definition) at landscape scales, and (2) use this framework to estimate the wetland indicator rating of *Picea pungens* Engelm. (Colorado blue spruce) across a large land area. We selected *P. pungens* as a test species because of its broad range, patchy local distribution, and the relatively low confidence in the existing rating that has been reported by wetland scientists. In addition, because of *P. pungens* often high contribution to local vegetation cover and current NWPL rating of FAC, it can be consequential to the outcome of wetland delineations and determinations using USACE methods. However, the main goal of our paper is to develop a general framework that, with appropriate species-specific modifications, can be used to quantify the indicator rating of any species on the NWPL.

Methods

Study Species and Study Area

Picea pungens is a large conifer tree discontinuously distributed in mountain regions of Arizona, New Mexico, Idaho, Utah, Colorado, and Wyoming (Little 1971). The current NWPL wetland indicator rating for the species is facultative (FAC) (Lichvar 2013), making it a hydrophyte for the wetland vegetation criterion in the USACE manual (Environmental Laboratory 1987). It can locally dominate mid-elevation mountain stream valleys throughout its range and its indicator rating can in part determine whether a site has hydrophytic vegetation for USACE wetland identification purposes. Regional floras and plant guides describe this species as occurring in streamside habitats (Weber and Wittmann 2012; Nelson and Williams 1992), but the species is also known to occur outside of riparian corridors as part of mixed conifer forests (Taylor 1993). Hybridization between *P. pungens* and *P. engelmannii*, a dominant of subalpine forests throughout the Rocky Mountains, may occur where the species' ranges overlap (Taylor 1993; Schaefer and Hanover 1985; Mitton and Andalora 1981).

Our study area was located in north-central Colorado and southern Wyoming, USA and encompassed 259 12th level Hydrologic Unit Basins (HUBs) occurring in the Northern Parks and Ranges Section of the Bailey ecoregion classification (Bailey 1980) and covering a total of 22,921 km^2 (Fig. 1). A distinguishing characteristic of our study area is a distinct north to south climate gradient, with southern HUBs having a more pronounced late-summer monsoon precipitation regime (Gutzler 2004; Higgins et al. 1997). This is reflected in differences in forest composition and structure from north to south in the region (Peet 2000) and has been found to influence the functioning of groundwater-dependent wetlands (Cooper 1990).

Species Distribution Modeling

Steep topography and low road density make sampling across mountain landscapes logistically challenging. In addition, the broad but patchy distribution of *P. pungens* across its range and the lack of detailed distribution maps pose additional challenges for developing effective sampling designs. Existing range maps by Little (1971) are at a scale too coarse (1:1,000,000) to efficiently direct a sampling program. Anecdotal accounts of *P. pungens*' distribution are found in regional floras (Weber and Wittmann 2012; Nelson and Williams 1992; Dorn 2001), but geospatial data at a suitable spatial scale are unavailable.

To develop a more targeted basis for sampling, we developed and compared several species distribution models (SDMs) and incorporated the best performing model into our sampling design. SDMs have been widely used to analyze rare species, model invasive plants, and predict responses to climate change and many well-tested algorithms have been developed (Wiens et al. 2009; Sousa-Silva et al. 2014; Gibson et al. 2014; Phillips et al. 2004; Elith and Leathwick 2009; Franklin 2010). Unlike these studies, our main motivation for SDM development was to help define a more efficient sampling frame.

We used occurrence records for *P. pungens* obtained from herbarium collections and vegetation plot data (n=401) as

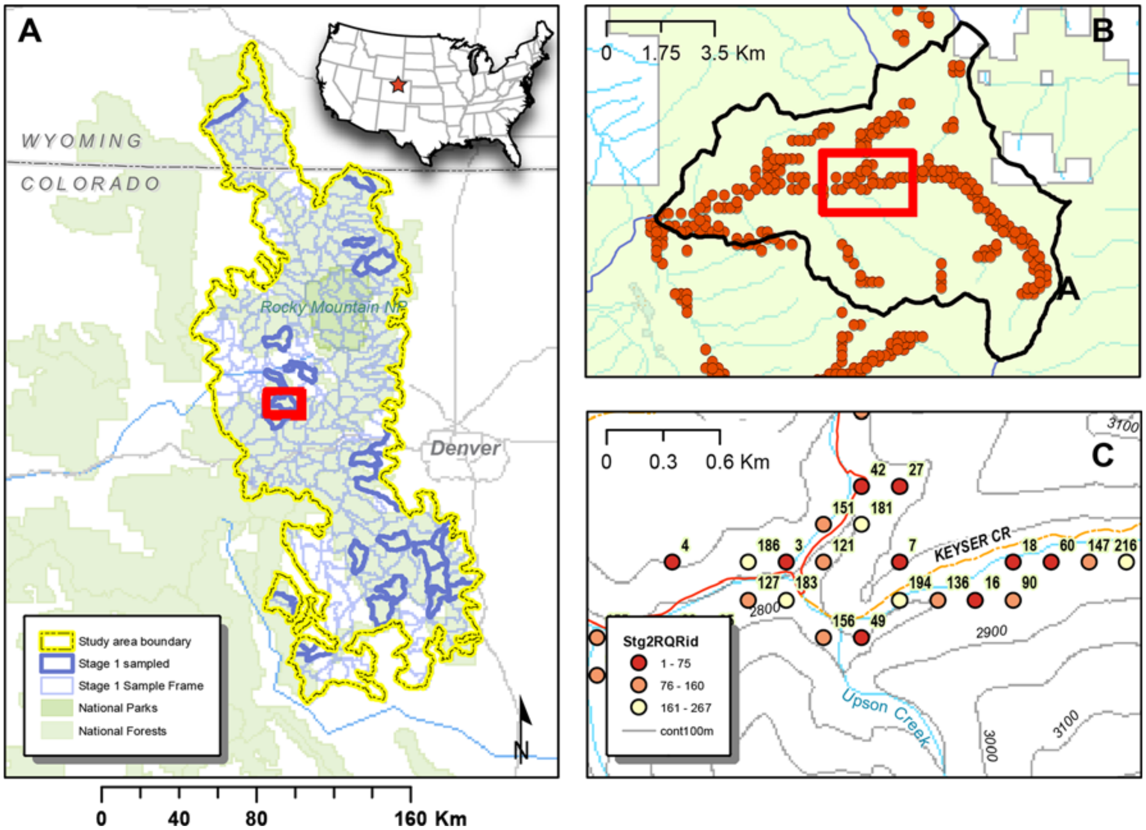

Fig. 1 Southern Rocky Mountain region study area (*panel A*, inset) illustrating assessment area boundary, 12th level HUBs, and selected first stage watersheds. Example of a 12th level HUB (*panel B*), and a close-up of selected stage 2 points (*panel C*)

inputs to derive SDMs, and used a range of environmental layers processed in ArcGIS (v. 10.2, ESRI, Inc.) including 30 m National Elevation Dataset (NED) elevations, NED-derived slope, and two NED-derived Topographic Position Index (TPI) layers as explanatory variables (see electronic supplement for more details on variables and data sources). TPI compares the elevation of raster cells to the mean elevation of a neighborhood specified around that cell (De Reu et al. 2013; Jenness et al. 2013; Weiss 2001), set in our analysis as 150 m and 600 m (5 and 20 cells, respectively). High positive TPI values represent areas that are higher than the mean of their surroundings, negative values represent locations in valleys, and TPI values near zero represent either flat areas or areas of constant slope (De Reu et al. 2013). Other explanatory variables used in SDM generation included modeled PRISM precipitation data (Daly et al. 2008; PRISM Climate Group 2014), and a distance to stream layer derived from stream centerlines in the National Hydrography Dataset (NHD).

Species distribution models were developed and evaluated using the Software for Assisted Habitat Modeling (SAHM) built on the VisTrails modeling platform (Morisette et al. 2013). SAHM allows users to simultaneously compare multiple SDMs generated from different algorithms, create continuous species prediction surfaces and binary presence/absence maps, and provides visualization and workflow management tools to assist in SDM development (Talbert and Talbert 2012). Processing modules in SAHM run algorithms in external programs (R, MaxEnt) for model creation and the production of diagnostic plots and statistics for evaluating model performance (Morisette et al. 2013; Talbert and Talbert 2012).

Five SDMs were developed using *P. pungens* occurrence data and explanatory variables. For model runs, 10,000 pseudo-random points were randomly generated across the modeling domain. Generalized linear models (GLM) were run using a bidirectional stepwise procedure and Akaike's Information Criterion (AIC) was used to compare model performance using different model parameters and covariates. The Multivariate Adaptive Regression Splines (MARS) algorithm, which fits piecewise logistic regression models, was also run using *P. pungens* presence/pseudo-absence data. Boosted Regression Trees (BRT) and Random Forests (RF), two ensemble machine learning algorithms based on classification and regression trees, were evaluated (Breiman 2001; Elith et al. 2008). SAHM uses the 'gbm' function in R to run the BRT model (Elith et al. 2008; Talbert and Talbert 2012), which starts with a single decision tree, and using a deviance reduction criterion and stepwise cross-validation procedure, evaluates the effect of incrementally added trees on error (Elith et al. 2011). Lastly, the SAHM module running Maximum Entropy software was used to develop a Maxent

SDM that minimizes relative entropy between the probability densities estimated for the species and that estimated for the available environment (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011).

Ten-fold cross-validation with a 70 % testing/training split was used to evaluate model performance. Calibration plots and statistics describing the goodness-of-fit between the predicted values and the observations of each of the five SDMs were used to identify model over or under fitting (Pearce and Ferrier 2000). Receiver operating characteristic curve (ROC) plots were used to examine the relationship between model sensitivity and specificity and to identify thresholds used to discretize continuous predictions of *P. pungens* occurrence into presence/absence rasters. Area under the curve (AUC) scores >0.8 indicate good model fit (Swets 1988; Talbert and Talbert 2012). We evaluated model confusion matrices describing model over and under prediction. Based on this information, we selected the RF SDM for use in subsequent sample design steps. See the electronic supplement for additional details regarding SDM development.

Sampling Design

To maintain inference to our entire study area yet maximize sampling efficiency, we implemented a multi-staged cluster design to allocate sampling resources (Fig. 2). For both the first stage (watersheds) and second stage (locations within watersheds), we used the Reverse Randomized Quadrant-Recursive Raster (RRQRR) algorithm in ArcGIS to generate a spatially-balanced sample list. An equitable spatial distribution of samples across the sample frame can improve statistical efficiency by maximizing spatial independence among sample locations (Theobald et al. 2007; Olsen et al. 2012).

HUBs intersecting the Northern Parks and Ranges ecoregion section comprised our initial sampling frame. To increase sampling efficiency, we eliminated HUBs with less than 10 % of their area supporting predicted *P. pungens* habitat on public lands. From this final sampling frame ($n=247$ HUBs), we used the RRQRR algorithm to develop an ordered list of HUBs for sampling. To decrease the likelihood of selecting HUBs that had no *P. pungens* populations, we used an unequal probability surface in our first stage selection. HUBs with known occurrence data (herbarium specimen locality records or vegetation plot data) were given a priority of 1, while those meeting the minimum threshold of predicted habitat and public lands but lacking historical records were given a priority of 0.3. The RRQRR algorithm produces a continuous ordered list of samples, and if a selected feature cannot be sampled because of inaccessibility or an absence of target populations, the next feature on the list is selected. Pilot sampling indicated that the final SDM over-predicted *P. pungens* occurrences, so an oversample list was created to allow for the replacement of HUBs lacking occurrences.

For the second stage of the sampling design, we used the RRQRR algorithm in ArcGIS to create sample points within selected HUBs (Fig. 2). *Picea pungens* is a common tree in some habitats, but it is uncommon across the study area as a whole. While the SDM reduced the need to search areas of clearly unsuitable habitat (e.g., alpine tundra), the patchy local distribution of *P. pungens* resulted in many instances where a selected sample area supported no trees. The study area's rugged terrain and low road density imposed high travel costs both between randomly selected points and for searching for *P. pungens* trees near selected points. In pilot sampling, we found that a search radius of approximately 100 m effectively balanced trade-offs between the time spent searching an area for the presence of a tree and not finding it and the additional travel cost imposed by abandoning a site as lacking *P. pungens* when it was present but outside the defined search radius. For each stage 1 HUB, a RRQRR point list was created for the entire sample frame, comprised of predicted habitat from the binary SDM, public lands within 300 m of roads or trails, and areas with slopes<25°. Because of the variability in watershed size, habitat characteristics, road density, and land ownership across the study area, the total number of points per HUB varied.

Field Sampling

Because of limited vehicle access within HUBs and natural terrain breaks, we subdivided the final stage 2 points into clusters with common road or trail access. Each cluster had a minimum of 5 RRQRR points with trees occurring within 1 km of each other. In every case, the lowest numbered point in each cluster was visited first, and the point with the next lowest number selected if *P. pungens* was not found at the first sample point. Each RRQRR point was the center of a 100 m radius search area within which field crews searched for *P. pungens*. Where multiple trees occurred within the search area, a laser range finder and GPS were used to identify the tree closest to the RRQRR point coordinate, thereby providing an objective basis for choosing the specific tree assessed. Within each stage 1 HUB, we sampled a minimum of 5 and maximum of 25 trees, eliminating HUBs where field reconnaissance indicated no *P. pungens* occurred or too few were present to reach the minimum sample size.

In higher elevation HUBs, it was critical to distinguish *P. pungens* from *P. engelmannii* where they co-occur. Several morphological characteristics including cone length and width, needle shape, and branching pattern were used to distinguish these species (Mitton and Andalora 1981; Schaefer and Hanover 1985; Weber and Wittmann 2012; Taylor 1993). It is unclear whether *P. pungens* and *P. engelmannii* hybridize (Mitton and Andalora 1981; Daubenmire 1972), so to avoid ambiguity in our analyses, we only sampled trees that clearly exhibited all *P. pungens* traits.

To determine the presence or absence of wetland hydrologic regime, we documented primary hydrologic indicators such as

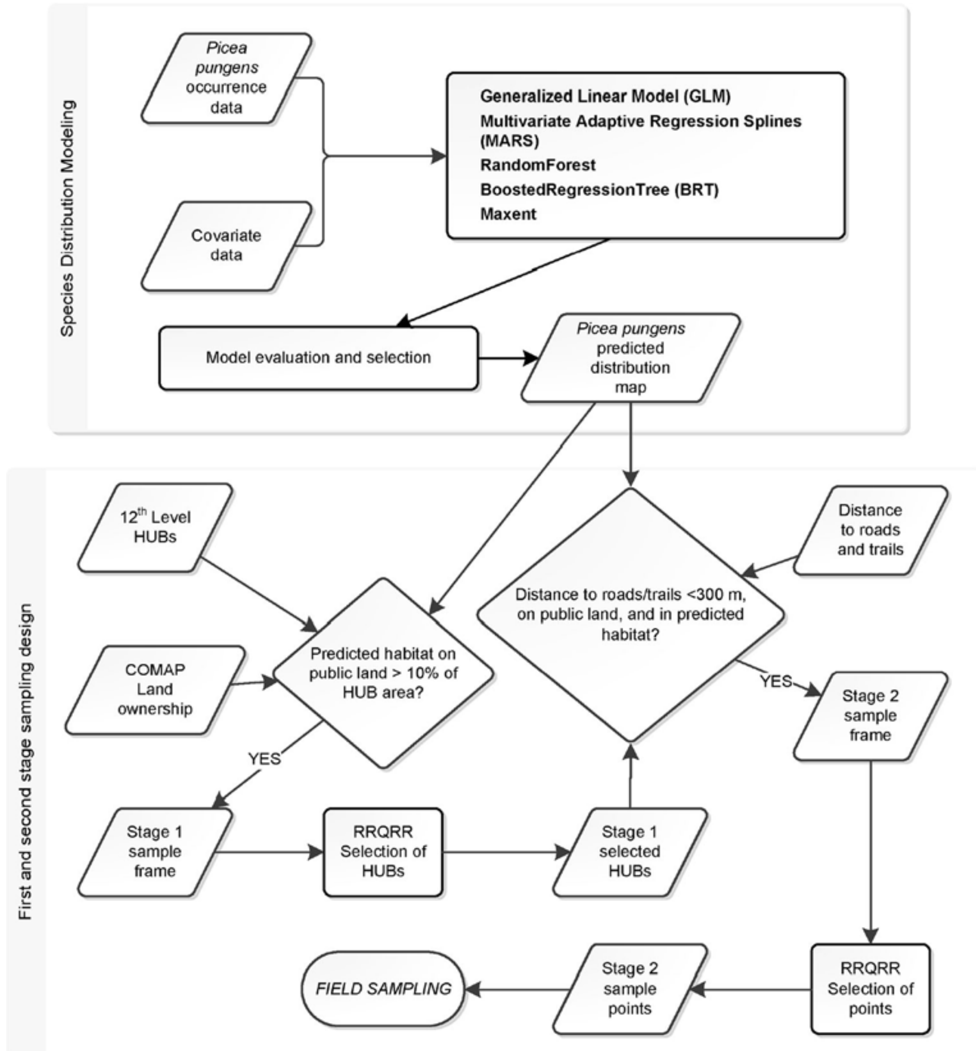

Fig. 2 Flowchart illustrating the main steps used in this study

surface water, water table depth, and other indicators described in the Regional Supplement to the Corps of Engineers Wetland Delineation Manual: Western Mountains, Valleys, and Coast Region (see Table 2 in the electronic supplement) (USACE 2010). At each site, we dug a 51-cm deep soil pit adjacent to the sampled *P. pungens* tree and as close to the base of the tree as possible, but offset as needed to avoid tree roots. Soils were evaluated for hydric soil indicators found in the WMVC Regional Supplement and the presence/absence of wetland hydrology and soil indicators recorded (USACE 2010).

Results

Species Distribution Modeling

The Random Forest (RF) and Boosted Regression Trees (BRT) SDMs had the highest predictive accuracy on training and cross validation data sets. The RF model had the highest mean area under curve (AUC) value, 0.83, for the cross validation folds. While all models performed reasonably well, evaluation of confusion matrices and AUC curves indicated that the RF model had the highest overall predictive accuracy on the holdout data (Table 1). The threshold probability value used for binary classification of the continuous RF prediction surface was set as the point where model sensitivity equaled model specificity (0.53). The RF model effectively captured the valley bottom and lower slope positions characteristic of *P. pungens* main habitat types, and the model was most strongly influenced by physiographic variables like TPI and elevation (Fig. 3). The most important variable in the model was distance to streams, followed by elevation and the courser-scale TPI layer (Fig. 3).

Field Sampling

Trees were sampled in 22 HUBs capturing the physiographic and ecological variability of *P. pungens* habitat across broad

Table 1 Summary of AUC values from cross-validation runs for different SDMs developed in this study

Model	n	Mean	Median	IQR	Min	Max	Training
BRT	10	0.82	0.82	0.03	0.78	0.86	*0.95*
GLM	10	0.73	0.74	0.05	0.64	0.78	*0.74*
MARS	10	0.77	0.80	0.06	0.70	0.83	*0.81*
Maxent	10	0.80	0.79	0.04	0.72	0.85	*0.84*
RF	10	0.83	0.83	0.02	0.80	0.88	*0.84*

latitudinal and elevation gradients and a variety of landscape positions (Fig. 4). Of the 423 *P. pungens* sampled, 70 (16.5 %) were in sites with hydric soil and wetland hydrology indicators and were considered wetlands. The remaining 353 trees (83.5 %) were in sites lacking these indicators and were considered uplands. The percentage *P. pungens* in each HUB occurring in wetlands was highly variable, ranging from 0 % in six HUBs, to 57 % in one HUB.

In general, HUBs in the southern portion of the study area had the lowest percentage of trees in wetlands. In these HUBS, *P. pungens* trees were common in mid-slope topographic positions as well as valley bottoms, whereas in the northern portion of our study area, trees were generally restricted to valley bottoms and lower slope positions. However, even in valley bottom and toe-slope positions, many sampled *P. pungens* were in locations that lacked wetland indicators.

Picea pungens would be assigned a rating of FAC (its current rating on the NWPL) in 5 HUBs, FACU in 11, and UPL in 6 (Fig. 4). Pooling our data, only 16.5 % of *P. pungens* trees were found in wetlands, which results in an indicator rating of FACU. In general, the frequency of *P. pungens* sampled in wetlands increased from south to north across our study area. This latitudinal pattern is correlated with the proportion of annual precipitation provided by summer monsoonal rains across the study area (Fig. 5). Indicator ratings assigned at the scale of individual HUBs showed a distinct trend with watersheds classified as UPL concentrated in areas with a greater proportion of annual precipitation occurring in July and August.

Discussion

The current wetland indicator rating for *P. pungens* on the NWPL in our study area is FAC (Lichvar 2013; USACE 2010), but our results suggest that an indicator rating of facultative upland (FACU) is more accurate. The high spatial variation in the relative frequency that *P. pungens* occurs in wetlands highlights an important conceptual difficulty in

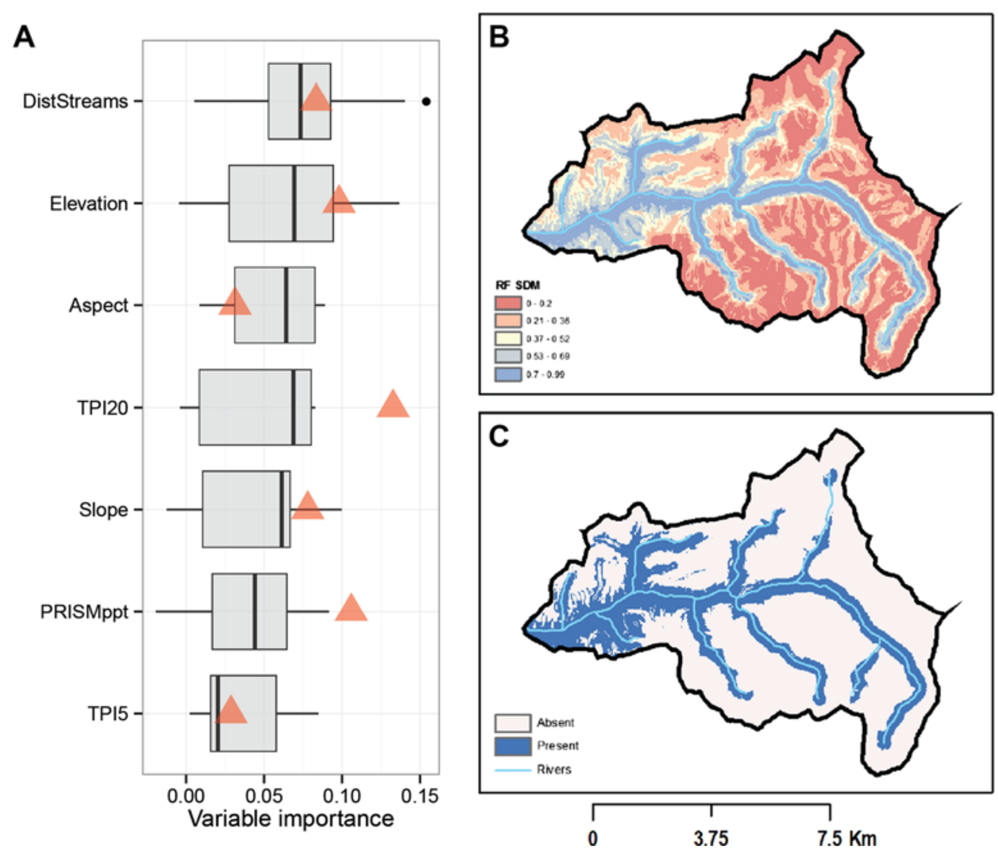

Fig. 3 Boxplots of variable importance measures (*panel A*) for Random Forest cross-validation runs (n=10) and training run (*triangles*). An example stage 1 HUB illustrating the Random Forest SDM as a continuous prediction surface (*panel B*) and discretized into a presence/absence layer using a threshold probability of 0.53 (*panel C*)

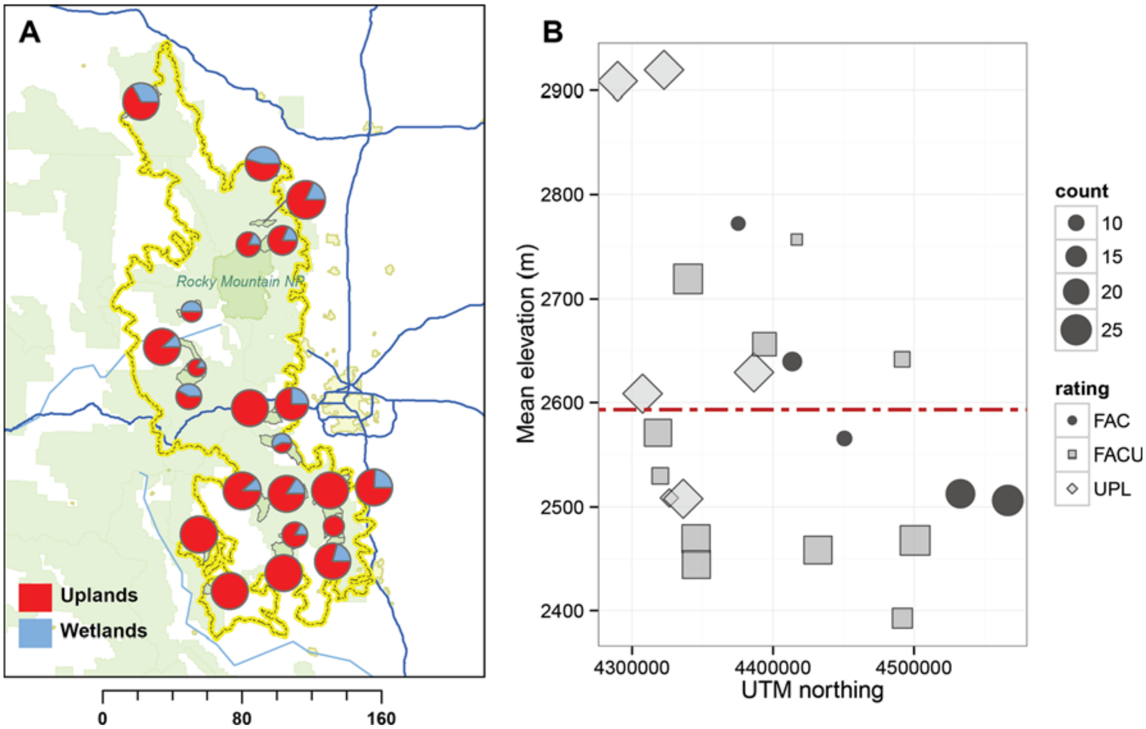

Fig. 4 Proportion of *P. pungens* trees sampled in wetlands and uplands for each stage 1 HUB; size of the pie corresponds to the number of trees sampled (*panel A*). Mean elevation, UTM northing, and estimated indicator rating of sampled watersheds; dashed line represents mean elevation of sampled trees across all watersheds (*panel B*)

using frequency-based ratings: the habitat affinities of many species varies geographically. This is recognized in the NWPL, which provides separate lists and species indicator ratings for each USACE region as well as some subregions. However, the NWPL regions are large and heterogeneous. The USACE WMVC region that includes our study area spans the entire Rocky Mountains, Cascade and Sierra Nevada ranges, and western coastal mountains and encompasses tremendous climatic and ecological variation.

In northern HUBs, *P. pungens* was largely limited to valley bottom locations, where wetlands more commonly occur, while in southern HUBs, trees occurred more frequently on slopes far from streams and riparian zones. We hypothesize that this may reflect differences in the strength and consistency of the summer monsoon precipitation pattern, which more strongly influences the southern portion of our study area (Kittel et al. 2002). Late summer rains may produce higher summer soil water contents, allowing *P. pungens* to expand out of the riparian zone and into mid-slope positions. The importance of monsoon precipitation in the southern part of the region has been demonstrated for such diverse phenomena as variations in subalpine tree line and water table dynamics in mountain fens (Anderson 2012; Fall 1997; Cooper 1990).

A primary goal of this study was to develop a generalizable approach suitable for quantifying the wetland rating of any plant species over a large geographic area. The USACE is developing mechanisms for challenging indicator ratings and our study provides a rigorous, statistically-based approach suitable for undertaking such analyses. Approximately 40 challenges to NWPL plant species ratings have occurred since 2012 when the list was first revised under Corps administration. Resolution of these cases was based primarily on expert opinion, but future challenges may benefit from a quantitative analysis like the one presented in this study.

When sampling species with broad ranges, multi-stage sampling designs can be useful, but the logistical challenges presented by sampling large areas require careful planning to allow for successful implementation. Efficient sampling must address uncertainties in what is known about the distribution of a species. Developing SDMs as in this study represents one possible approach, but if accurate habitat or range maps are available, this step may not be necessary or desirable given the complexity it adds.

The broad spatial extent of our sample frame allowed us to make statistically-grounded statements about the frequency of occurrence of *P. pungens* in wetlands over a large geographic area. However, we have no statistical inference to populations in other parts of the WMVC region. *Picea pungens* is found across a large area of the southern Rocky Mountains and the adjacent southwest, and our results suggests that it likely occupies significantly different habitats in the northern and southern portions of its range.

A critical challenge in sampling a species with a discontinuous distribution like *P. pungens* is efficiently locating plants

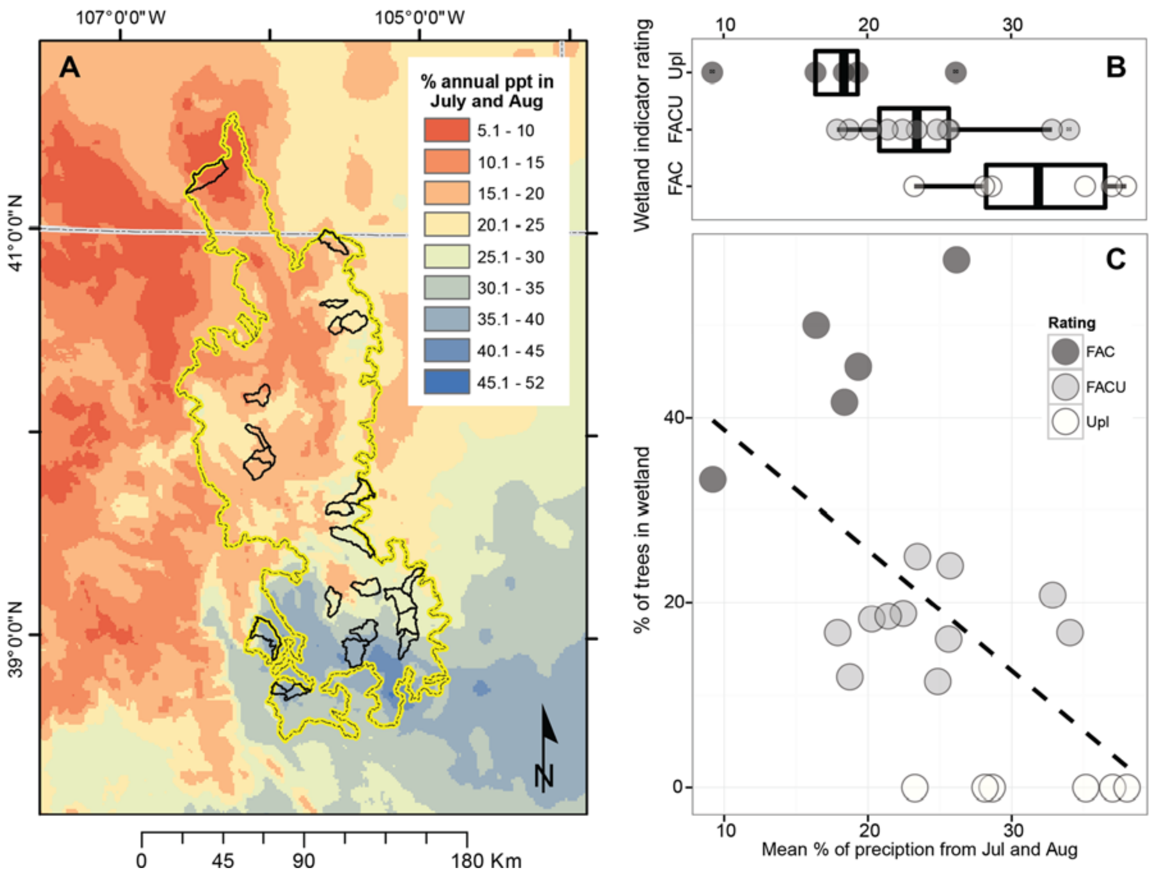

Fig. 5 Map of the proportion of annual precipitation from the months of July and August (PRISM 1981–2010 normals; *panel A*); mean proportion of annual precipitation from July and August for each HUB binned into wetland indicator rating classes (*panel B*); percent of trees in wetlands for watersheds along a gradient of late summer precipitation (*panel C*; linear trend line added for reference)

for sampling. Considerable time was spent searching for *P. pungens* in areas where it was absent because our SDM over-predicted its occurrence. Because absences play no part in the calculation of frequencies, over-prediction introduced no bias in our final estimates, but it did reduce sampling efficiency. This is preferable to the use of an overly restrictive SDM that could introduce bias if areas incorrectly omitted from the sample frame disproportionately occur in either wetlands or uplands.

The results from any SDM are best viewed as hypotheses to be iteratively tested and validated with new data (Jarnevich et al. 2015). Although we are in a better position after field sampling to produce a more accurate SDM for *P. pungens*, our SDM served its intended purpose in contributing to a more efficient sampling design. We attribute over-prediction in our SDMs to several factors, including biases in the occurrence data used to create the models. Many botanists collect specimens of well-known taxa such as *P. pungens* only when the identity of a plant is in question or the population is an unusual occurrence, representing a possible source of geographic bias that can complicate model interpretation (Aiello-Lammens et al. 2015; Hijmans 2012; Graham et al. 2004).

Our decision to limit the sampling frame to areas proximate to roads may be a source of geographic bias, although we see no a priori reason why this should be so. Most roads in our study region were originally developed from old trails or wagon roads and occur in relatively low landscape positions, paralleling valley bottoms. Although untested in our analysis, we believe that if any biases were introduced by our constraining the sample frame, it would be towards areas more likely to support wetlands than not.

The main motivation for incorporating species distribution modeling into our sampling design was to eliminate the considerable portion of our study area that lacks *P. pungens* habitat. Large elevation gradients drive patterns of ecosystem zonation in the southern Rockies (Daubenmire 1943) and sampling approaches that fail to recognize this will be highly inefficient, limiting their effectiveness at large scales. While the RF model chosen from our model selection process over predicted the extent of *P. pungens* habitat, it achieved its purpose of narrowing our sample frame enabling us to sample at landscape scales.

To our knowledge, this is the first study to characterize a species' wetland indicator rating at such a broad scale.

However, the regions used to assign ratings on the NWPL are significantly larger in extent and more heterogeneous in character. This study cannot provide statistical inference to unexamined portions of *P. pungens* range, but our results do suggest that ratings at such broad spatial scales would be difficult to test. As our study demonstrates, wetland indicator values can vary at geographic scales much smaller than those now used to assign NWPL ratings.

Conclusions

We present an objective method for quantifying the wetland indicator rating of a plant species. Our general approach could be useful for developing new ratings for critical plant species or for use in future updates to existing NWPL ratings. All NWPL wetland ratings were originally assigned by best professional judgment, and while empirical data cannot realistically be collected for all species on the NWPL, we demonstrate that it is feasible to quantitatively assign ratings for individual species even at broad landscape scales.

Acknowledgments Funding for this study was provided by the U.S. Environmental Protection Agency, U.S. Fish and Wildlife Service, and the U.S. Army Corps of Engineers under the Wetland Regulatory Assistance Program (WRAP). Special thanks to Dr. Anthony Olson of EPA, Western Ecology Division, for discussions related to our sampling design and methods. Thanks to Joanna Harter, Sven Bultema, Dan Kotter, and Amanda Snyder for assistance in the field and to Mary Butterwick for input on study objectives and design. Thanks also to Catherine Jarnevich for help with species distribution modeling.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38(5):541–545

Anderson L (2012) Rocky mountain hydroclimate: holocene variability and the role of insolation, ENSO, and the North American monsoon. Glob Planet Chang 92–93:198–208

Bailey RG (1980) Description of the Ecoregions of the United States. USDA Forest Service, Washington, D.C

Breiman L (2001) Random forests. Mach Learn 45:5–32

Cooper DJ (1990) Ecology of Wetlands in Big Meadows, Rocky Mountain National Park, Colorado. U.S. Fish and Wildlife Service, Washington, D.C

Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris PP (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int J Climatol 28(15):2031–2064

Daubenmire RF (1943) Vegetational zonation in the Rocky Mountains. Bot Rev 9(6):325–393

Daubenmire R (1972) On the relation between Picea pungens and Picea engelmannii in the Rocky Mountains. Can J Bot 50(4):733–742

De Reu J, Bourgeois J, Bats M, Zwertvaegher A, Gelorini V, De Smedt P, Chu W, Antrop M, De Maeyer P, Finke P (2013) Application of the topographic position index to heterogeneous landscapes. Geomorphology 186:39–49

Dorn RD (2001) Vascular plants of Wyoming. Mountain West Publishing, Cheyenne

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40(1):677–697

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77(4):802–813

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17(1):43–57

Fall PL (1997) Timberline fluctuations and late quaternary paleoclimates in the southern Rocky Mountains, Colorado. Geol Soc Am Bull 109(10):1306–1320

Franklin J (2010) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge

Gibson J, Moisen G, Frescino T, Edwards T Jr (2014) Using publicly available forest inventory data in climate-based models of tree species distribution: examining effects of true versus altered location coordinates. Ecosystems 17(1):43–53

Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT (2004) New developments in museum-based informatics and applications in biodiversity analysis. Trends Ecol Evol 19(9):497–503

Gutzler DS (2004) An index of interannual precipitation variability in the core of the North American monsoon region. J Clim 17(22):4473–4480

Higgins RW, Yao Y, Wang XL (1997) Influence of the North American monsoon system on the U.S. summer precipitation regime. J Clim 10(10):2600–2622

Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93(3):679–688

Jarnevich CS, Stohlgren TJ, Kumar S, Morisette JT, Holcombe TR (2015) Caveats for correlative species distribution modeling. Ecol Inform 29:6–15

Jenness J, Brost B, Beier P (2013) Land facet corridor designer: extension for ArcGIS. Jenness enterprises. Available at: http://www.jennessent.com/arcgis/land_facets.htm

Kittel TG, Thornton PE, Royle JA, Chase TN (2002) Rocky mountain climates: historical and future patterns. In: Baron J, Ehrlich PR (eds) *Rocky mountain futures: an ecological perspective*. Island Press, Washington, D.C

Laboratory E (1987) Corps of engineers wetlands delineation manual. U.S. Army corps of engineers. Waterways Experiment Station, Vicksburg

Lichvar RW (2013) The National Wetland Plant List: 2013 wetland ratings. Phytoneuron 49:1–241

Lichvar RW, Minkin P (2008) Concepts and procedures for updating the National Wetland Plant List. U.S. Army Engineer Research and Development Center and Cold Regions Research and Engineering Laboratory, Hanover

Lichvar RW, Butterwick M, Melvin NC, Kirchner WN (2014) The National Wetland Plant List: 2014 update of wetland ratings. Phytoneuron 41:1–42

Little EJ (1971) Atlas of United States Trees. Volume 1, Conifers and Important Hardwoods. US Department of Agriculture, Washington DC

Mitton JB, Andalora R (1981) Genetic and morphological relationships between blue spruce, *Picea pungens*, and Engelmann spruce, *Picea engelmannii*, in the Colorado Front Range. Can J Bot 59(11):2088–2094

Morisette JT, Jarnevich CS, Holcombe TR, Talbert CB, Ignizio D, Talbert MK, Silva C, Koop D, Swanson A, Young NE (2013) VisTrails SAHM: visualization and workflow management for species habitat modeling. Ecography 36(2):129–135

Nelson RA, Williams RL (1992) Handbook of Rocky Mountain Plants. Roberts Rinehart Publishers, Niwot

Olsen AR, Kincaid TM, Payton Q (2012) Spatially balanced survey designs for natural resources. In: Gitzen RA, Millspaugh JJ, Cooper AB, Licht DS (eds) Design and Analysis of Long-Term Ecological Monitoring Studies. Cambridge University Press, Cambridge, pp 126–150

Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. Ecol Model 133(3): 225–245

Peet RK (2000) Forests and meadows of the Rocky Mountains. In: North American Terrestrial Vegetation, vol 2. Cambridge University Press, New York, pp 75–122

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2):161–175

Phillips SJ, Dudík M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. In: Proceedings of the twenty-first international conference on Machine learning. ACM, p 83

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190(3):231–259

PRISM Climate Group (2014) Data extracts of 30-year annual temperature and precipitation normals (1981–2010). Oregon State University PRISM Climate Group. http://prism.oregonstate.edu

Reed PB (1988) National list of plant species that occur in wetlands: National summary. USDI Fish and Wildlife Service, Washington D.C

Schaefer PR, Hanover JW (1985) A morphological comparison of Blue and Engelmann Spruce in the Scotch Creek drainage, Colorado. Silvae Genet 34:2–3

Sousa-Silva R, Alves P, Honrado J, Lomba A (2014) Improving the assessment and reporting on rare and endangered species through species distribution models. Glob Ecol Conserv 2:226–237

Swets, J (1988) Measuring the accuracy of diagnostic systems. Science 240: 1285–1293

Talbert C, Talbert M (2012) User Documentation for the Software for Assisted Habitat Modeling (SAHM) package in VisTrails. US Geological Survey, Fort Collins

Taylor RJ (1993) Picea. In: Flora of North America Editorial Committee (ed) Flora of North America North of Mexico, vol 2. Oxford University Press, New York

Theobald DM, Stevens DL Jr, White D, Urquhart NS, Olsen AR, Norman JB (2007) Using GIS to generate spatially balanced random survey designs for natural resource applications. Environ Manag 40(1): 134–146

Tiner RW (1999) Wetland indicators : a guide to wetland identification, delineation, classification, and mapping. Lewis Publishers, Boca Raton

Tiner R (2006) Lists of potential hydrophytes for the United States: a regional review and their use in wetland identification. Wetlands 26(2):624–634

Tiner RW (2012) Defining hydrophytes for wetland identification and delineation. U.S. Army Corps of Engineers, U.S. Army Engineer Research and Development Center, Cold Regions Research and Engineering Laboratory, Washington, D.C

USACE (2010) Regional supplement to the corps of engineers wetland delineation manual: western Mountains, Valleys, and Coast Region (Version 2.0). U.S. Army Engineer Research and Development Center Environmental Laboratory, Vicksburg

Weber WA, Wittmann RC (eds) (2012) Colorado Flora: eastern slope, 4th edn. University Press of Colorado, Niwot

Weiss A (2001) Topographic position and landforms analysis (Poster Presentation). Paper presented at the ESRI Users Conference, San Diego, CA

Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proc Natl Acad Sci U S A 106:19729–19736