Ecological Modelling 414 (2019) 108836

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Various measures of potential evapotranspiration have species-specific impact on species distribution models

Arjun Adhikari[a,d,*], Kumar P. Mainali[b,e], Imtiaz Rangwala[c], Andrew J. Hansen[a]

[a] 310 Lewis Hall, Department of Ecology, Montana State University, Bozeman, MT 59717, United States
[b] National Socio-Environmental Synthesis Center (SESYNC), University of Maryland, 1 Park Pl Suite 300, Annapolis, MD 21401, United States
[c] CIRES/Western Water Assessment, University of Colorado, 325 Broadway, R/PSD NOAA ESRL, Boulder, CO 80305, United States
[d] Department of Natural Resource Ecology and Management, Oklahoma State University, OK 74078
[e] Conservation Innovation Center, Chesapeake Conservancy, Annapolis, MD 21401, United States

ARTICLE INFO

Keywords:
PET
Penman-Monteith
Thornthwaite
Habitat suitability
Conservation

ABSTRACT

The growth and distribution of plant species in water limited environments is often limited by the atmospheric evaporative demands which is measured in terms of potential evapotranspiration (PET). While PET estimated by different methods have been widely used to assess vegetation response to climate change, species distribution models offer unique opportunity to compare their efficiency in predicting habitat suitability of plant species. In this study, we perform the first multi-species comparison of two widely used metrics of PET i.e., Penman-Monteith and Thornthwaite, and show how they result in similar or different on projected distribution of water limited species and potential consequences on their conservation strategies across North Central U.S. To build species distribution models of eight species, we used two sets of environmental predictors which were identical except for the metric of PET (Penman-Monteith vs Thornthwaite) and projected habitat suitability for historical (2005) and future (2099) periods. We found an excellent model performance with no difference under two sets of predictors (AUC = ~0.93). The relative influence of Thornthwaite PET on habitat prediction was higher than Penman PET for most of the species. We observed that the area of the projected suitable habitat was always higher under Thornthwaite set of predictors than Penman set of predictors (ranges from 25 % to 941 %), with the exception of *Pinus contorta* for which the reverse was true. In most cases, these differences were non-trivial, indicating that the choice of the PET metric, although both of them are commonly used, can have dramatic consequences on the conservation management decisions. Therefore, the conservation management decisions can be markedly different depending on the choice of the PET metric used for species distribution modeling of water limited species.

1. Introduction

Species distribution models (SDMs) are widely used tools for projecting distribution of species under climate change and for estimating the relative impact of various predictors of distribution (Chang et al., 2014; Guisan and Thuiller, 2005; Mainali et al., 2015; Piekielek et al., 2015). Hence, SDMs may offer an opportunity to compare the relative importance of two different measures of the same underlying phenomenon. To date, most SDM applications have used one formulation of potential evapotranspiration (PET), i.e., Thornthwaite, for projecting habitat suitability of species under the climate change (Chang et al., 2014; Dilts et al., 2015). This widely used formulation of PET is based only on temperature. A new formulation of PET called Penman-Monteith includes additional metrics for estimating PET. As PET estimated by these two metrics differ in a given space, it is reasonable to expect that the projected suitable habitat also differs depending on the metric of PET. In this study, we explore how two common methods of PET estimation can have different impacts on habitat projections and potential consequences on conservation efforts of water limited species across north central U.S.

Atmospheric evaporative demand often plays the dominant role in structuring the vegetation communities in water limited environment (Currie, 1991; Li et al., 2013). This demand, called PET, has been estimated with several methods such as Penman-Monteith (Monteith,

* Corresponding author. Current address: Department of Natural Resource Ecology and Management, 008C Agricultural Hall, Oklahoma State University, Stillwater, OK 74078, United States.
E-mail addresses: arjun.adhikari@okstate.edu (A. Adhikari), kmainali@umd.edu (K.P. Mainali), imtiaz.rangwala@colorado.edu (I. Rangwala), hansen@montana.edu (A.J. Hansen).

https://doi.org/10.1016/j.ecolmodel.2019.108836
Received 21 April 2019; Received in revised form 21 September 2019; Accepted 2 October 2019
Available online 15 November 2019

1965; Penman, 1948), Thornthwaite (1948); Priestley and Taylor (1972), and Turc (1961). As different methods result into different PET values, the choice of PET in modeling approaches may result in different ecological interpretations. However, the common approaches of estimating PET include Penman-Monteith method (hereafter Penman) and Thornthwaite method (hereafter, Thornthwaite). Because Thornthwaite PET can be computed with temperature alone, it has had wider applications. Alternatively, Penman method requires several additional variables, viz solar radiation, relative humidity, vapor pressure deficit, and wind speed. Although it provides a more sophisticated model of PET, a reliable estimation of PET with Penman has largely been a formidable challenge in past, especially at large spatial extents, primarily because of lack of available metrics at such spatial extents. The latest generation of GCMs, however, provide key elements required to estimate Penman PET, i.e. solar radiation, vapor pressure deficit, and wind speed (Abatzoglou and Brown, 2012; Stocker et al., 2013; Taylor et al., 2012), making it easier than before to compute the PET.

Comparison of the two metrics of PET has shown considerable variation in space. Some have found higher Penman PET compared to Thornthwaite PET and others found the opposite (Fisher et al., 2011; Hobbins et al., 2008; Lu et al., 2005; Van Der Schrier et al., 2011). A global comparison found that PET estimates by Thornthwaite are higher than Penman in the tropics and lower in the subtropics (Van Der Schrier et al., 2011). Lower PET values derived from Thornthwaite types method compared to Penman method have been reported for the USA (Fisher et al., 2011; Vörösmarty et al., 1998) and Sub-Saharan Africa (Hulme et al., 1996). In a recent study, Adhikari et al. (2019) estimated lower Thornthwaite PET than Penman PET along a strong water balance ecotone across north central U.S. Compared with Thornthwaite, Penman formulation of PET validated reasonably well against field data in regional and global scale studies (Benli et al., 2010; Chen et al., 2005; López-Urrea et al., 2006; Tukimat et al., 2012; Weiß and Menzel, 2008). The greater reliability of Penman PET values is thought to be due to a more sophisticated model of PET with several variables, which is expected to estimate the actual physical process more reliably than a simpler Thornthwaite model of PET does (Lu et al., 2005). Because of their wider use and noticeable differences, it is necessary to compare the effects of PET derived from these two methods for ecological and management applications.

Because the two methods are substantially different in estimated PET, various indices derived from these PET (e.g., variation in aridity index, Palmer's drought index, and moisture index) should also vary considerably between Penman and Thornthwaite (Dewes et al., 2017). Consequently, this Penman-Thornthwaite discrepancy can have adverse impacts on strategies, plans, and processes for climate change adaptation (McAfee, 2013). Therefore, the choice of PET must be guided by objective evaluation of the alternate methods that provide an estimate of PET. For instance, future studies could project the less extreme loss of habitat suitability of water-limited species under Thornthwaite PET due to less atmospheric evaporative demands under Thornthwaite PET.

Past studies have demonstrated considerable difference in habitat predictions resulting from different algorithms, spatial resolutions, global climate models, predictors, sample sizes, and climate change scenarios (Acevedo et al., 2017; Araújo and Guisan, 2006; Bucklin et al., 2015; Henderson et al., 2014; Hernandez et al., 2006; Mainali et al., 2015; Pearson et al., 2006; Syphard and Franklin, 2009, 2010; Thuiller et al., 2004). However, model performance and projections of habitat suitability of species mostly influenced by moisture stress under Penman vs. Thornthwaite PET have not been evaluated yet. Particularly, the choice of PET estimated by an appropriate method can be of highly impactful in projecting suitable habitat in water-limited environment. Therefore, the choice of PET in SDM of water-limited species can influence policy-guiding efforts for conservation and management of species under current and future climates. In this study, we compare the impact of Penman and Thornthwaite PET in projecting the habitat suitability of eight dominant tree species in water-limited forest ecosystems of north central U.S. Specifically; we aim to answer the following scientific questions in this study:

1 Does the performance of models built under the Penman PET set of predictors better explain distributions of water-limited tree species than those built under Thornthwaite PET set (the two sets keep identical set of predictors except for PET)?
2 To what extent does the weighting of environmental predictors differ in models using the Penman vs. Thornthwaite formulation of PET?
3 How does projected area of suitable habitat for water limited species under climate change differ under the two metrics of PET?

2. Methods

2.1. Study area and species

North central U.S. is our study region that spans from Washington at north-west to Michigan at north-east and from Nevada at south-west to Tennessee at south-east; the study region is 3,495,769 km^2 of the contiguous U.S. and it includes over twenty-five states (Fig. 1). The region

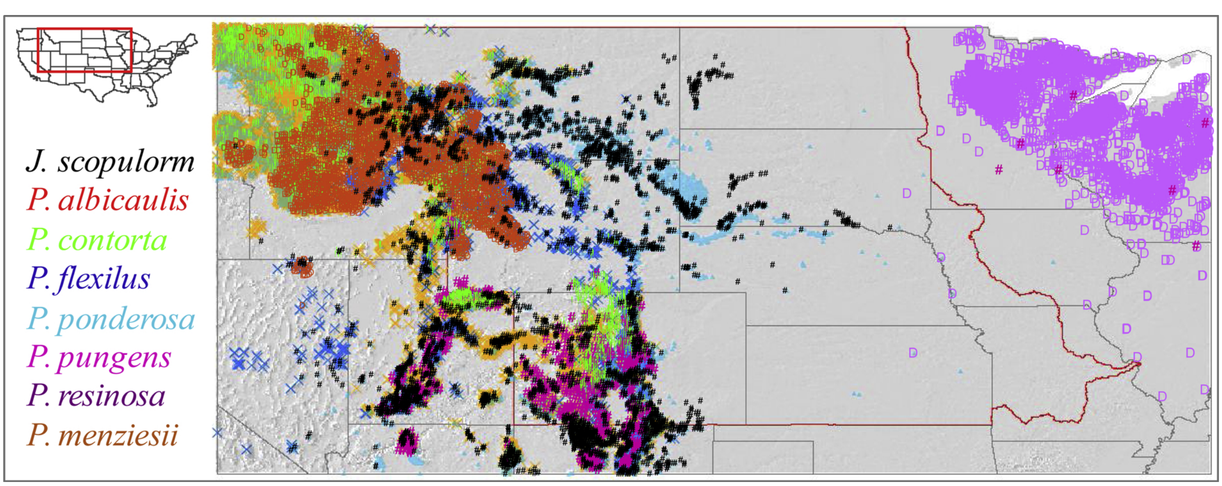

Fig. 1. Map showing study area (North Central U.S.) and Forest Inventory Analysis (FIA) records of species presence. Red box represents the North Climate Science and Adaptation Center domain. Color of species presence records in the map corresponds the color assigned for the texts of species name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

is characterized by strong environmental gradients from drier west to high humid east due to gradients in temperature and precipitation. The region comprises eight major forest communities with the following dominant tree species: Doulas fir (*Psuedotsuga menziessi*), Ponderosa pine (*Pinus ponderosa*), Aspen (*Populus* sp.), Black spruce (*Picea* sp.), Hemlock (*Tsuga* sp.), Whitebark pine (*Pinus albicaulis*), and Red maple (*Acer rubrum*). Many forest ecosystems of this region are under various degrees of exposure to the climate change. To study the difference in influence of Penman PET and Thornthwaite PET on habitat modeling, we selected eight dominant tree species, viz., *Juniperus scopulorum, Pinus contorta, Pinus flexilis, Pinus ponderosa, Pinus resinosa, Pinus albicaulis, Pinus pungens* and *Psuedotsuga menziessi,* that (1) exist in relatively dry region of north central U.S., and (2) have their growth and distribution strongly limited by water availability.

2.2. Distributional data

We derived presence and absence records of each species from the U.S. FIA program database (http://apps.fs.fed.us/fiadb-downloads/datamart.html). The FIA has delineated the forest of our entire study area into a grid of hexagonal cells that are 2500 ha (= 25 km^2) each. In each grid cell is one long-term sampling plot composed of four adjacent circles of 58.9 ft (~18 m) radius each. A census on the trees is conducted inside these circles. This systematic and through sampling across the U.S. provides a high-quality data about tree distribution. The absences were drawn from the grid cells that did not contain the species in FIA data. To reduce the chances of false absences, we added a buffer of 5 km around each presence point and excluded any absences falling within this buffer. Our approach of (a) identifying areas of absences with thorough sampling and (b) excluding absent records within 5 km radius of a presence point is expected to provide high quality data for species distribution models because the absent records are more likely to represent an absent state compared to a typical SDM where pseudoabsences are drawn. For a regression model like Random Forest we used, two categories of the data represent contrasting states of presence and absence although modelers conveniently use the term "pseudoabsences" for the background data. This collectively indicates that our models are more informed as they operate on environmental space of presences vs true absences.

The delineation of geographic background for obtaining absences can dramatically impact the model performance and estimated habitat suitability. Specifically, a large background can artificially inflate model evaluation score such as AUC and simultaneously give a model that does a poor job of discriminating sites for suitability in the core region of distribution (Acevedo 2012). Therefore, we adopted local convex hull approach to determine the geographic background where a model is trained. A local convex hull of presences eliminates larger areas within minimum convex polygon without occurrence records, thereby shrinking the background. For each species, we tried a range of local convex hull with different alpha parameters and selected the one that was substantially smaller than minimum convex polygon but included enough areas to contrast grid cells with presences in environmental space. Because we use a regression model (Thuiller et al., 2016) that builds SDM by contrasting environmental space of presences with that of absences (when the absences do not fall in the grid cells with presences), we included an equal number of presence and absence records to the model.

2.3. Historic climate data

Environmental predictors including monthly average minimum and maximum temperature, precipitation, PET, and relative humidity, solar radiation, and wind speed for the entire United States at 4 km spatial resolution were derived from Multivariate Adaptive Constructive Analogs (MACA) products. Available predictors in MACA data have been derived by a statistical downscaling method and calibrated with observed meteorological dataset (i.e. training dataset) from several weather stations to make compatible spatial patterns after correcting historical biases. These predictors are available through webpage of University of Idaho (https://climate.northwestknowledge.net/MACA/) (Abatzoglou and Brown, 2012). MACA data incorporates daily data from general circulation models and validated over western United States by global reanalysis data. The advantage of MACA data over other downscaled data includes the following: 1) MACA avoids interpolation based methods with the use of analogs, and 2) MACA's multivariate approach to improve the physical relationships among the variables (Abatzoglou and Brown, 2012). The 4 km spatial resolution data was again statistically downscaled to 1 km spatial resolution. Available PET estimates in MACA product was computed with Penman-Monteith method using solar radiation, humidity, and wind velocity data. A subset of each predictor was created with a shape file of our study area (Fig. 1). Monthly average Thornthwaite PET was estimated using monthly average temperature from MACA products following a method described in Chang et al. (2014). All the historic climate data were summarized as monthly average for the period of 1980-2006.

2.4. Non climate predictors

In addition to the climatic variables, we used aridity index, available water holding capacity (AWHC), and % sand (Miller and White 1998) as non climatic predictors to project habitat suitability of species.

2.5. Collinearity analysis

Eighty-seven predictors were initially considered for each species for constructing SDMs. For a given species, the only predictor that was different between Penman and Thornthwaite set was the measure of PET: Penman PET vs Thornthwaite PET before the collinearity analysis. Highly collinear predictors do not uniquely contribute to the model but such a collinearity among predictors can be problematic when assessing significance of individual parameters. Therefore, we eliminated highly correlated predictors of each species from the set using Software for Assisted Habitat Modeling (SAHM) embedded in the VisTrails scientific workflow management system (Morisette et al., 2013). Specifically, for each species, we eliminated predictors from the set such that the remaining covariates have a Pearson's correlation coefficient of <0.70. Since this was performed for each species separately, the final set of predictors for each species was different. However, different species do not necessarily have the same collinearity between two predictors. This set of predictors was paired with (1) Penman PET to create one set of predictors (hereafter, Penman set), and with (2) Thornthwaite PET to create another set of predictors (hereafter, Thornthwaite set). The differences in the habitat suitability estimates with the use of Penman set and Thornthwaite set would be the unique effect of Penman PET and Thornthwaite PET when several other predictors are included as predictors.

2.6. GCM and future climate data

To understand impacts of warming under climate change from 2071 to 2099, we adopted two climate change scenarios with the same set of climate variables projected by general circulation model (GCM). Selected two climate change scenarios include high and low representative concentrative pathway (RCP8.5 and RCP4.5) from 2010 to 2099. The RCP 8.5 scenario represents the amount of anthropogenic forcing of 8.5 W/m^2 consistent with increases in atmospheric greenhouse gases at current rates whereas RCP 4.5 represents anthropogenic forcing of 4.5 W/m^2, a significant reduction in global greenhouse emissions (Moss et al. 2010). For each of these two emission scenarios, the future climates were created by averaging their prediction for the period of 2071–2099 from a warm and dry CCSM4 GCM. Both historical and future environmental variables are similar, but future ones are projected under climate change scenarios. The CCSM4 GCM moderately captures overall spread of future projections of temperature and precipitation changes across the study area (Adhikari and Hansen, 2019; Adhikari et al., 2019).

2.7. Species distribution models

To model species distribution, we used Random Forest (RF) implemented in Biomod2 software programmed in R environment (Thuiller et al., 2016) as it is one of the most efficient modeling methods used in species distribution modeling (Magness et al., 2008; Mainali et al., 2015). Often single decision tree (or, classification and regression tree, CART) may end up with high variance and high biases. Contrary to CART, the advance extension of RF builds multiple decision trees using subsamples of available input variables; this makes the model more stable with better generalization and higher predictive power of independent data (Breiman, 2001). RF has been found in omitting noises in the input variables to improve accuracy and control over-fitting (Matsuki et al., 2016).

2.8. Model development and evaluation

Since no independent dataset was available, the presence/absence data of each species was randomly split in a ratio that 80 % data have been used for model development/calibration and 20 % data have been used for model evaluation with 5-fold cross-validation (Dormann et al., 2012). The calibration and evaluation selection was run for 100 times before analysis the result. The accuracy of the model was assessed from the data generated by the split-sample using two metrics: area under the curve (AUC) of receiver operator characteristic (ROC) curves and true skill statistic (TSS). These two metrics consider different weights associated with various types of prediction errors of omission, commission or confusion. Widely reported AUC metric is both threshold and prevalence independent model evaluation metric (Fielding and Bell, 1997). Models with the AUC value < 0.70 is considered as poor, 0.7-0.9 as moderate and > 0.9 a good model. TSS is threshold dependent metrics for model evaluation which ranged between -1 (no agreement) and 1(total agreement) (Landis and Koch, 1977). We interpreted TSS statistics as < 0.4 were poor, 0.4-0.8 useful, and > 0.8 good to excellent. R script of the analysis is included in supplement.

2.9. Analysis

We compared AUC and TSS scores secured by the best models created from Penman set vs Thornthwaite set. The study also compared the relative influence of the predictors on habitat predictions of each species under two sets of predictors.

We categorized probability or habitat suitability into two categories as below: suitable (greater than 0.50) and unsuitable (less than 0.50). We then assessed the ratio of the suitable area predicted by Penman set to the Thornthwaite set.

3. Results

Each species ended up with different numbers of predictors for model trainings after removing autocorrelated predictors (Fig. 2). Interestingly, the final set of predictors of a species were very similar in the two sets of PET. Available water holding capacity and soil texture (percent sand) were common predictors among all species.

Our results showed no difference in performance of the models constructed with the two sets of predictors (Table 1). Overall, the models under both sets (Penman and Thornthwaite) of predictors secure good to excellent score in prediction, with the AUC and TSS values ranging from 0.93 to 0.98 and 0.71 to 0.85 respectively (except that AUC was 0.84-0.86; TSS was 0.58-0.61under both sets of predictors for *P. pungens*). AUC is a popular metric of model evaluation when a model needs to be evaluated for both false positive and false negative (a situation that is not typical of traditional ecological analysis but definitely a concern in SDM). This metric is highly intuitive to modelers. Therefore it has a wider application in SDM work. However, studies have shown many times that AUC can be unreliable in certain conditions (e.g., Lobo et al., 2008; Mainali et al., 2015). To minimize this challenge, we employed alpha hull of presences for selecting absences. Also, the design of the study (true absences) would mean that AUC should reflect true underlying model performance, which is in contrast to a typical SDM where the background points are used as pseudoabsences. This made us confident that AUC is the right choice of model evaluation and we stuck to it because scientific community is more comfortable to this metric. To add to our analysis, we also computed TSS score. These two model evaluation scores are strongly correlated with $R^2 = 0.96$. This indicates that the traditionally reported problems with AUC are virtually absent in our study. Therefore, we reported the model output of habitat suitability based on widely used AUC.

Among the environmental predictors, precipitation had highest influence on habitat distribution of all species except *P. resinosa* under Penman PET set (Fig. 2). However, Thornthwaite PET showed highest influence on predicting habitat of all species except *P. resinosa* under Thornthwaite set. Therefore, as the most dominant pattern in influential predictors, Thornthwaite set identifies Thornthwaite PET itself as the most influential predictor whereas Penman set identifies predictors other than the measure of PET as the most influential predictors. Under both sets of predictors, soil texture (% sand) was the most influential factor for the distribution of *P. resinosa* (Fig. 2). Available soil water holding capacity showed some degree of influence on the habitat distribution of *P. contorta*, *P. flexilis, P. resinosa* and *P. menziesii* (Fig. 2). Under both set of predictors, solar radiation from March to July showed some influence over the distribution of *J. scopulorum*, and *P. menziesii*. May to September precipitation showed considerable impacts on distribution of *J. scopulorum*, *P. flexilis*, *P. ponderosa*, *P. albicaulis* and *P. menziesii* under both sets of predictors (Fig. 2). January precipitation showed the greatest impacts on distribution of *P. pungens* under both PET. Interestingly, the influence of precipitation on habitat prediction of all species was lower under Thornthwaite set than under Penman set; it is easy to see that this difference is offset by the difference in influence of the metric of PET itself.

A total of 48 separate maps of habitat suitability (Fig. 3) were generated for 8 species * 3 climate scenarios (current, RCP4.5, RCP8.5) * 2 sets of predictors (Penman and Thornthwaite). The extent of suitable habitat under current climate was predicted higher by Thornthwaite set than Penman set for five species, viz. *J. scopulorum, P. ponderosa, P. resinosa, P. menziesii*, and *P. pungens* (Figs. 3–5, Table 2). All of these species except *P. resinosa* showed a marked decline in suitable habitat in future, with the difference between Penman and Thornthwaite remaining similar as under current climate. For two species (*P. albicaulis* and *P. flexilus*), predicted current habitat was similar under both Penman and Thornthwaite but they diverge in future, showing similar effect as in the other species (i.e., Thornthwaite predicting larger extent than Penman). The only species that exhibited larger extent predicted by Penman than Thornthwaite under any climate is *P. contorta*. The percentage change in habitat of all species in future compared to current prediction are listed in Table 3. Overall, Thornthwaite set predicted larger extent of suitable habitat than Penman set did for all scenarios (current, RCP 4.5, RCP 8.5) of all species with two exceptions: (1) the prediction was similar for *P. albicaulis* and *P. flexilis* under current climate, and (2) the predictions are in reverse direction (Penman > Thornthwaite) for *P. contorta* under all climate (Fig. 5).

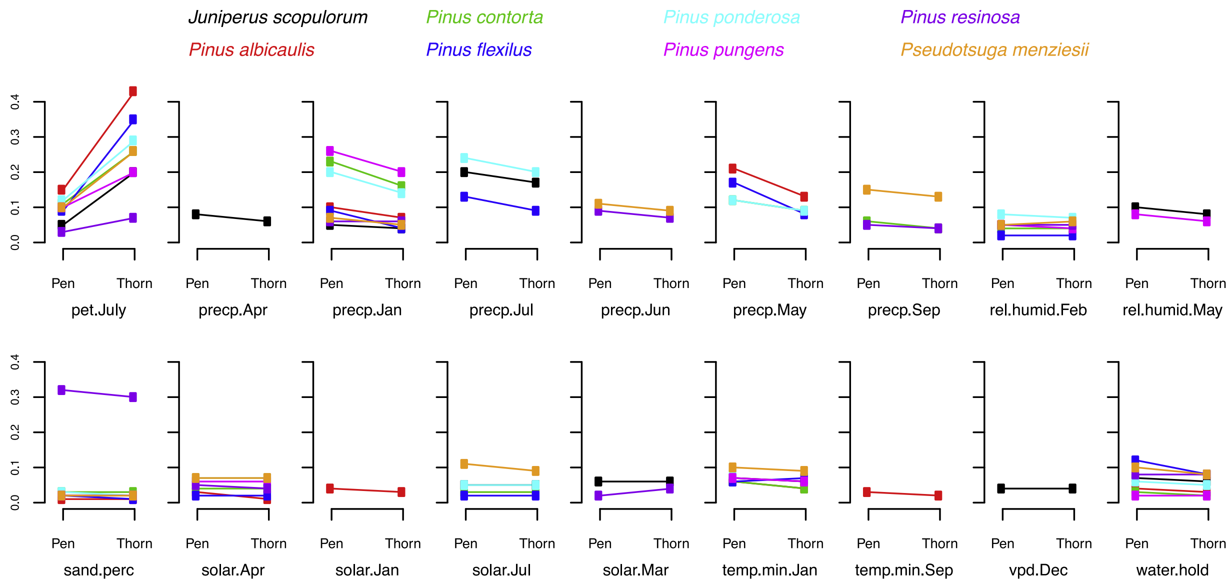

Fig. 2. Comparison of relative importance score of each of the predictors under Penman and Thornthwaite sets. Each panel shows one predictor (listed on x-axis). The left cluster of points represent importance of the variable when it was included in Penman set and the right cluster in Thornthwaite set for eight species (in different color). A line connecting same colored circles on the Penman and Thornthwaite set reflects how the variable contributed explanatory power in the two sets of predictors. For example, a positive slope indicates that the variable has higher influence under Thornthwaite set than in Penman set, and vice versa. Because highly correlated predictors were eliminated sequentially for each species separately, the final set of predictors to enter the model was unique for the species.

Table 1
Evaluation scores for each species under two set of predictors: Area under ROC curve (AUC), and True skills statistics (TSS). Note: PenAUC and PenTSS represent AUC and TSS scores under Penman set of predictors. ThornAUC and ThornTSS represent AUC and TSS scores under Thornthwaite set of predictors.

Species	PenAUC	PenTSS	ThornAUC	ThornTSS
J. scopulorum	0.93	0.72	0.93	0.72
P. contorta	0.98	0.85	0.97	0.85
P. flexilus	0.93	0.71	0.93	0.72
P. ponderosa	0.97	0.82	0.97	0.82
P. resinosa	0.97	0.84	0.97	0.84
P. menziesii	0.93	0.72	0.93	0.72
P. albicaulis	0.94	0.76	0.95	0.79
P. pungens	0.84	0.58	0.86	0.61

4. Discussion

Various metrics of potential evapotranspiration (PET) have been used in studies related to ecology, conservation, biogeography, climate change, etc where the choice of PET metric is apparently driven more by convenience and less by justification. Given that each metric of PET is specific in its parameters and model structure, the measure of PET is metric specific. Though a thorough comparison of different metrics on species distribution has never been tested, projected species distributions have been used in various kinds of management decisions and research questions. Here we perform the first multi-species comparison of two widely used measures of PET and show how they result in similar or different projection of species distribution.

Additional novelties of our study includes the following: (1) This is the first ever application of Penman-Monteith estimate of PET in species distribution modeling; (2) We downscaled MACA variables to a spatial resolution that is ecologically relevant to tree species distribution. MACA product is special in that it offers many non-standard climatic variables for future that are not available from other sources; and (3) We applied our model across a continental water-balance ecotone where the spatial pattern of water limitation emphasizes the need to represent PET adequately in modeling efforts. Collectively, our study makes a case for future modeling efforts of tree species distributions using a metric of PET that is more appropriate for the studied system and geographical area.

In this study, we compared influenced of PET estimated by two methods on habitat suitability of eight dominant tree species of north central US region, which is mostly driven by moisture stress. For each species, we predicted the habitat suitability with two sets of identical environmental predictors under Penman and Thornthwaite PET where the only difference is in the metric of PET (different species can have different set of predictors). This design of keeping all the predictors constant and varying only one predictor of interest (PET) allows us to directly and quantitatively compare the relative importance of two measures of PET (Penman vs Thornthwaite). Because the metric of PET is one of the most important predictors of the species distribution in moisture limited environment, the estimated importance of the PET as predictor is interpretable as a measure of variable importance that is unique to PET when all the other predictors (correlated and uncorrelated to PET) are also included in the model. Because these two metrics are commonly used estimates of PET, the discrepancy between the two models in projecting species distribution will have important consequences in conservation and restoration planning. Their difference in relative influence indicates the unique contribution of the metric in explaining species distribution. We show that the distribution of these species is projected substantially differently under Penman PET vs. Thornthwaite PET metrics. However, the predictive performance of models built with two sets of predictors was similar within a species.

The accuracy of current modeling method is high, showing good to excellent model performance under AUC model evaluation metrics, and the two sets of predictors do not differ in model performance. However, the observed dissimilarities in species distribution projections could be due to the impacts of limiting factors on growth and distribution of plant species which are captured differently by the regression models built based on Penman set of predictors vs Thornthwaite set of predictors. (e.g. sandy soil explained higher variability in habitat projection of *P. resinosa*). The interpretation of high performance of the models has some important caveats. First, the model performance metric is relevant only to model training and testing areas. The region of model projection can be much larger. Beyond the geographic space of model construction, the evaluation metric is irrelevant, and models with very high evaluation metric in the model construction range can

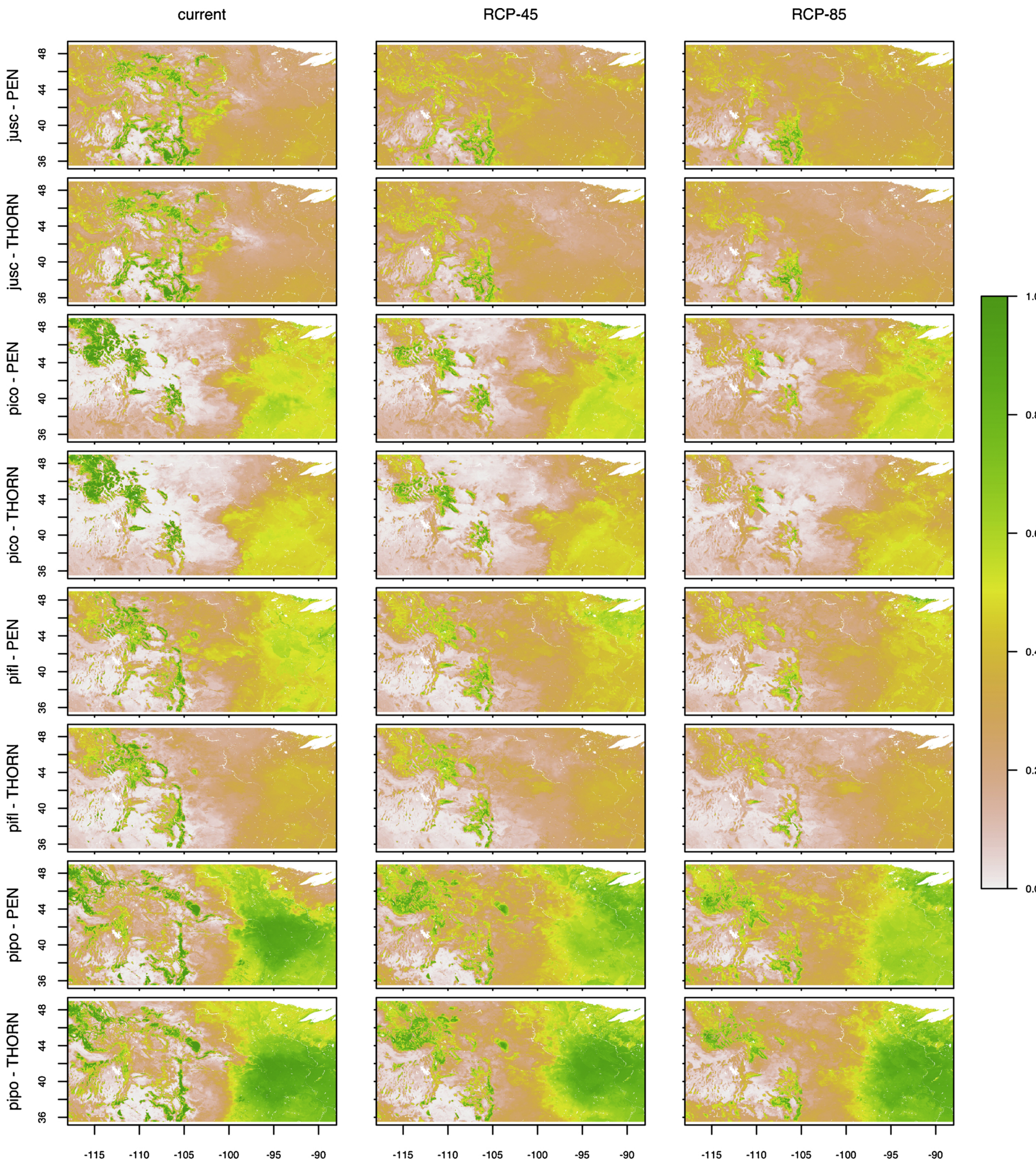

Fig. 3. Probability distribution maps of all species under current and future climates (RCP4.5 and RCP8.5 scenarios for 2099) as predicted by two sets of predictors, viz. Penman and Thornthwaite sets of variables. (Abbreviation, PEN: Penman; thorn: Thornthwaite; jusc*: Juniperus scopulorum,* pial: *Pinus* albicaulis, pico*: Pinus contorta,* pifl*: Pinus flexilis,* pipo*: Pinus ponderosa,* pire*: Pinus resinosa,* pipu: *Pinus pungens,* psme: *Pseudotsuga menzeisii*).

yield an unrealistic model for projecting far from the training area (Mainali et al., 2015). Second, a good fit of model with current distribution does not necessarily indicate the similar performance in the future (Porfirio et al., 2014). The underlying statistical relationship between environmental factors and suitable habitat of the species may change over time. These two types of challenges collectively indicate that the spatial (first challenge) and temporal (second one) stability of the species distribution models may not be as good as we desire, and unfortunately, our study can have both types of challenges.

AUC has been criticized as an unreliable metric of model evaluation metric in SDM with valid reasons (Lobo et al., 2008; Mainali et al., 2015). It is sensitive to geographic background (Lobo et al., 2008); it is entirely possible to secure a very high AUC and yield a useless model (Acevedo, 2017). Our study design is different from a traditional SDM study and so does not suffer from the same problems reported elsewhere for the following reasons. First, we do not use pseudoabsences; we have real absences collected by a long-term systematic data collection effort of large institutions that have well set standards. Second, contrary to a standard SDM that uses a convex hull, we shrank the background by using alpha hull. Third, our approach does a fair job in

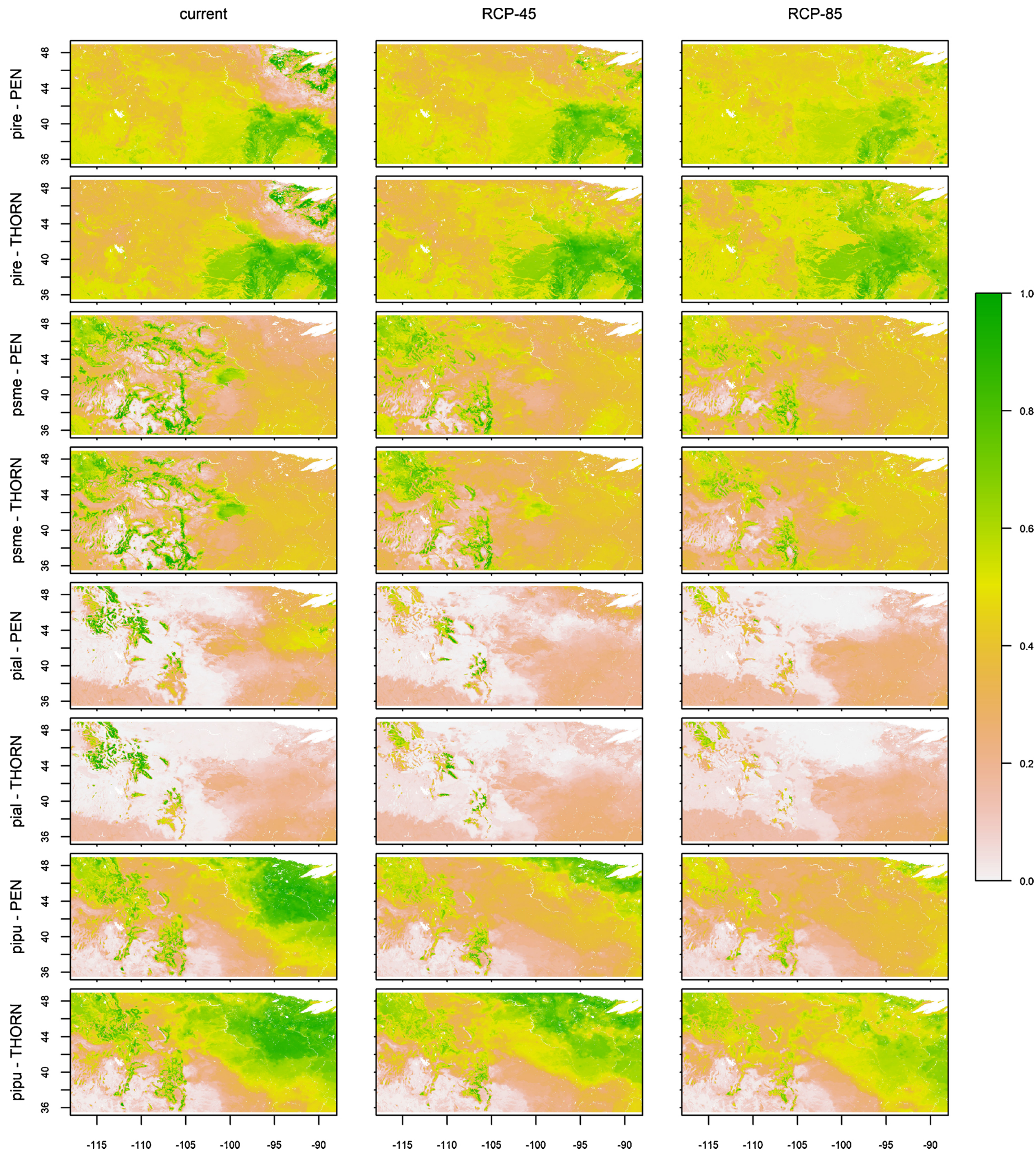

Fig. 3. (*continued*)

comparing the models because the Penman vs Thornthwaite set of predictors were supplied with the same set of presence-absence data including x-fold split of points into training and testing set. In such situations, even when the absolute value of AUC is not reliable, the relative difference is an indicator of model fit to data. Therefore, we have confidence in our results based on models evaluated with AUC.

Using eight tree species of water limited environment, we have demonstrated that uncertainties associated with methodological issues of important variables can affect model outputs substantially. This is not a situation of missing out an important predictor. Rather, this is an issue of two different approaches of estimating an important predictor, which is PET. A sub-optimal choice of the model for estimating PET may lead into erroneous planning for conservation and management of targeted species. Although, no past studies explicitly considered the issues on variation in habitat prediction due to difference in PET from two methods, our study suggests that the discrepancies in model outputs of different species have been associated with the sets of predictors under Penman and Thornthwaite PET. Among eight species considered for this study, the model showed that the predicted habitat suitability was higher under Thornthwaite set for current and both climate change scenarios than for Penman set for all species except *P. contorta*. Since many past studies reported lower PET values estimated by Thornthwaite method (Adhikari et al., 2019; Fisher et al., 2011; Hulme et al., 1996), the habitat suitability of water limited species under the

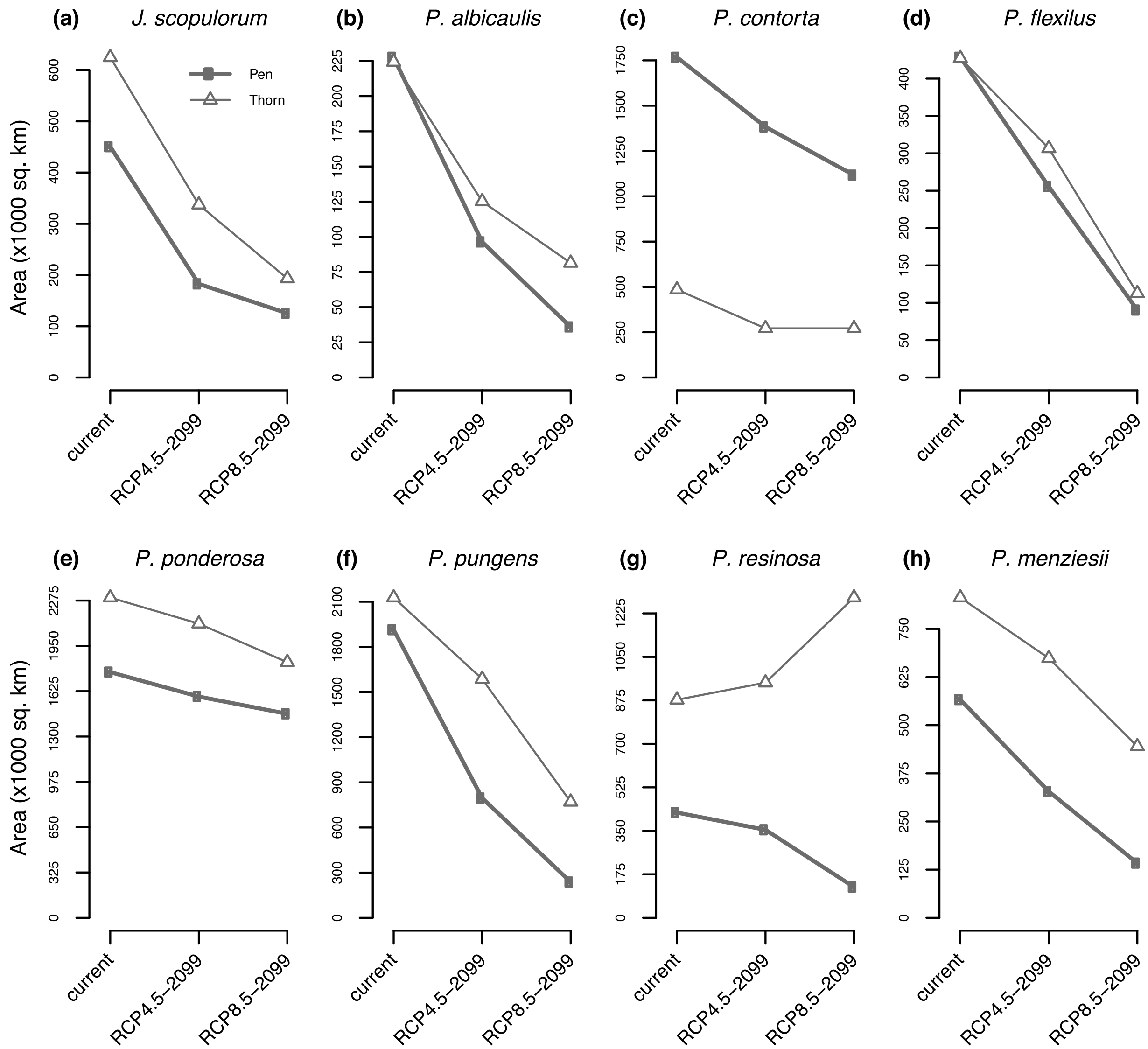

Fig. 4. Area of species range of each species under current and future climates (in 2099) projected by RCP4.5 and RCP8.5 climate change scenarios. Each panel shows comparison of suitable habitat area predicted by Penman and Thornthwaite sets of predictors.

influence of Thornthwaite PET should be over predicted because of low atmospheric evaporative demands under Thornthwaite method.

This study showed that difference in estimation method of the identical predictors (here PET) can alter influence of other variables on modeling outputs. In this study, the unique contribution of precipitation in explaining species distribution is higher under Penman set for most of the species. For example, under the Penman set, July precipitation was the most important predictor of the habitat of *P. flexilis, P. ponderosa,* and *J. scopulorum* but this was replaced by July PET with the Thornthwaite set. This may be due to the change in the extent of collinearity between the predictors when multiple methods produce different outputs for the same predictors. In addition, this variation is contingent upon the species types, environmental conditions, and geographical locations (Acevedo et al., 2012; Syphard and Franklin, 2009). The contribution of temperature on distribution is lower for all species; given that these species grow in water limited environments, it is not surprising to see a lesser role of temperature in determining distribution. However, the impacts of other variables are similar under both sets of predictors showing less importance on distribution of water limited plants.

4.1. Management and conservation implications

The consideration of potential range of a species for conservation and management depends upon the predictive ability of models for habitat suitability and identification of appropriate environmental predictors. Discrepancies in model predictions due to different sets of environmental predictors can impair the conservation and resource management planning. For example, it is important to be cautious during formulation of management plans for *P. resinosa* as the model predicted decreases in suitable habitat under Penman set and increases under Thornthwaite set. This species can be categorized as highly vulnerable when habitat is predicted under Penman PET set. Hence the study suggests for a careful consideration of model outputs generated by using appropriate predictors. As several other studies have shown that Penman estimate of PET is more reliable than Thornthwaite (López-Urrea et al., 2006; Weiß and Menzel, 2008; Benli et al., 2010), these prior studies can be a guide for selecting appropriate set of predictors even for species for which the future predictions are markedly different between Penman vs. Thornthwaite set.

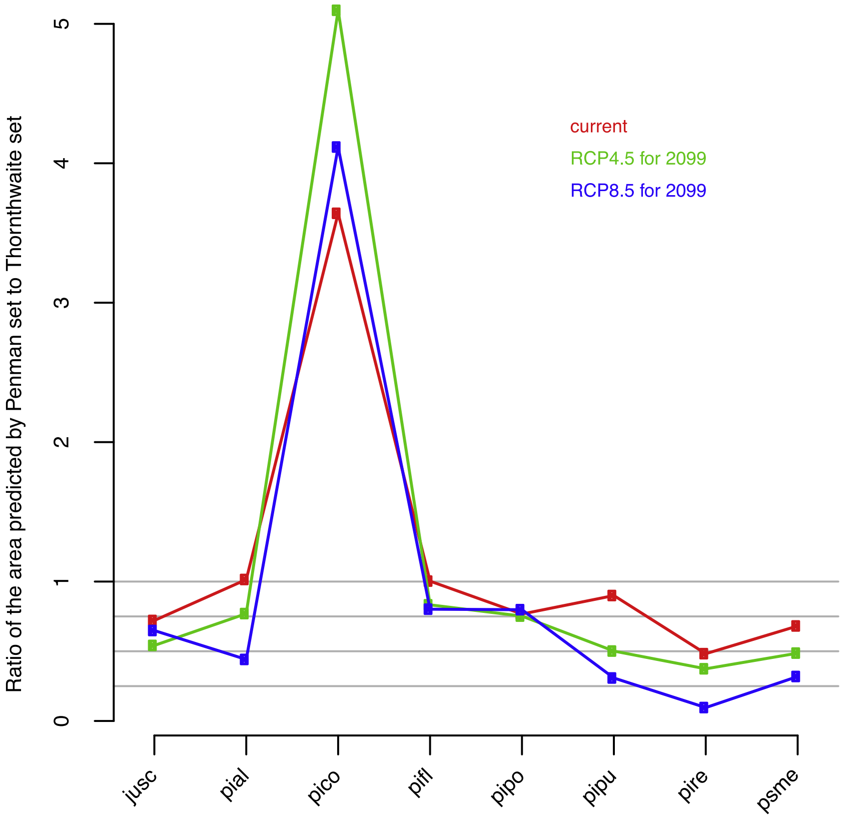

Fig. 5. Ratio of the suitable habitat area predicted by Penman set to Thornthwaite set for suitable habitat under current climate as well as RCP4.5 and RCP 8.5 climate change scenarios. A ratio of >1 indicates that Penman set of predictors project bigger area of species range than Thornthwaite does. (Abbreviation; jusc*: Juniperus scopulorum,* pial: *Pinus* albicaulis, pico*: Pinus contorta,* pifl*: Pinus flexilis,* pipo*: Pinus ponderosa,* pire*: Pinus resinosa,* pipu: *Pinus pungens,* psme*: Pseudotsuga menzeisii*).

5. Conclusion

Penman and Thornthwaite are commonly used measures of PET. These two measures are substantially different in model structure and complexity. Whereas Penman is considered to represent PET more accurately than Thornthwaite, the latter has wider availability. In this study, we performed a litmus test of how these two metrics of PET perform in predicting species distribution of eight species from moisture stress environment. For entire species range, Thornthwaite predicted higher area than Penman in most of the cases (climatic scenarios of eight species), and the differences are non-trivial. Hence, it is important to indicate that (1) the two metrics of PET are substantially different in predicting species range or highly suitable habitat, and (2) these differences are not uniform across species, i.e., one or the other metric of PET can predict higher suitable area for different species. Therefore, the conservation management decisions can be markedly different depending on the metric of PET used for SDM. It is important to emphasize that the ease of availability should not drive the use of Thornthwaite PET. Neither should the model complexity of Penman should make it more desirable. Whereas a more complex formulation of Penman PET might be better able to characterize the actual PET because of its associated several additional variables, a careful comparison of the two metrics in a given area and study systems would yield most accurate projection of species distribution.

Table 3
Percent change in species range in future compared to current range. The changes are reported for Penman set ("PenSpRange") and Thornthwaite set ("ThornSpRange") of predictors for each of the two climate change scenarios separately: RCP4.5 ("Change4.5") and RCP8.5 ("Change8.5").

Species	PenSpRange Change4.5	PenSpRange Change8.5	ThornSpRange Change4.5	ThornSpRange Change8.5
J. scopulorum	−59.44	−72.18	−46.03	−69.08
P. flexilus	−40.38	−78.93	−28.21	−73.64
P. ponderosa	−9.97	−16.98	−8.15	−20.19
P. resinosa	−16.38	−70.77	7.85	46.86
P. Menziesii	−42.12	−74.95	−18.95	−46.49
P. albicaulis	−64.411	−79.762	−44.216	−63.70
P.pungens	−58.44	−87.60	−25.42	−63.788
P. contorta	−21.74	−36.80	−44.10	−72.54

Table 2
Aerial extent of suitable habitat (in km^2) for each species under Penman and Thornthwaite sets. Note: _Pen, _Thorn represent under Penman and Thornthwaite set of predictors, respectively.

Species	Current_Pen	Current_Thorn	RCP4.5_Pen	RCP4.5_Thorn	RCP8.5_Pen	RCP8.5_Thorn
J. scopulorum	450,425	624,878	182,704	337,277	125,316	193,216
P. contorta	1,766,815	485,274	1,382,681	271,265	1,116,585	271,265
P. flexilus	428,465	427,169	255,450	306,653	90,273	112,610
P. ponderosa	1,761,741	2,296,307	1,586,167	2,109,136	1,462,664	1,832,729
P. resinosa	423,371	877,361	354,007	946,205	123,737	1,288,507
P. Menziesii	566,263	831,140	327,784	673,665	141,861	444,749
P. albicaulis	227,574	224,311	96,355	125,129	35,934	81,431
P.pungens	1,913,907	2,127,396	795,491	1,586,616	237,377	770,378

Author's contribution

Each author has made significant contribution. AA designed study, developed methods, analyzed data, and wrote and review the manuscript. KP built the model, analyzed the data, wrote and review the manuscript. IR wrote the method and review the manuscript. AJH designed study, wrote and review the manuscript.

Declaration of Competing Interest

The authors declare that there is no conflict of interest.

Acknowledgements

The study was funded and supported by U.S. Department of Interior North Central Climate Science Center (G14AP00181). We greatly appreciate the thoughtful and constructive comments made by two anonymous reviewers to improve this manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2019.108836.

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