



Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush

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Forecasting of species and ecosystem responses to novel conditions, including climate change, is one of the major challenges facing ecologists at the start of the 21st century. Climate change studies based on species distribution models (SDMs) have been criticized because they extend correlational relationships beyond the observed data. Here, we compared conventional climate-based SDMs against ecohydrological SDMs that include information from process-based simulations of water balance. We examined the current and future distribution of *Artemisia tridentata* (big sagebrush) representing sagebrush ecosystems, which are widespread in semiarid western North America. For each approach, we calculated ensemble models from nine SDM methods and tested accuracy of each SDM with a null distribution. Climatic conditions included current conditions for 1970–1999 and two IPCC projections B1 and A2 for 2070–2099. Ecohydrological conditions were assessed by simulating soil water balance with SOILWAT, a daily time-step, multiple layer, mechanistic, soil water model. Under current conditions, both climatic and ecohydrological SDM approaches produced comparable sagebrush distributions. Overall, sagebrush distribution is forecasted to decrease, with larger decreases under the A2 than under the B1 scenario and strong decreases in the southern part of the range. Increases were forecasted in the northern parts and at higher elevations. Both SDM approaches produced accurate predictions. However, the ecohydrological SDM approach was slightly less accurate than climatic SDMs (–1% in AUC, –4% in Kappa and TSS) and predicted a higher number of habitat patches than observed in the input data. Future predictions of ecohydrological SDMs included an increased number of habitat patches whereas climatic SDMs predicted a decrease. This difference is important for understanding landscape-scale patterns of sagebrush ecosystems and management of sagebrush obligate species for future conditions. Several mechanisms can explain the diverging forecasts; however, we need better insights into the consequences of different datasets for SDMs and how these affect our understanding of future trajectories.

Effects of recent climate change on species are reported for many ecosystems (Parmesan and Yohe 2003, Menzel et al. 2006) and include responses in species interactions, phenology, distribution, and abundance (Shafer et al. 2001, Gilman et al. 2010). Forecasting the effects of future climate change on species is essential to inform natural resource management and conserve ecosystem biodiversity (Jackson et al. 2009, Wiens et al. 2009). Important, and uncertain, elements of climate change include the magnitude of change in climatic conditions and the response of species, populations and ecosystems. In particular, ecological forecasting of these responses of the biota to novel situations needs to be improved considerably (Thuiller et al. 2005, Hijmans and Graham 2006, Zimmermann et al. 2009).

Species distribution models (SDMs) are valuable tools for investigating how species and ecosystems may respond to future climates because they statistically characterize the relationship between species occurrence and climatic conditions (Hijmans and Graham 2006, Elith and Leathwick 2009, Franklin and Miller 2009). SDMs extrapolate species

distribution data in space and time based on a statistical model between species occurrence data and environmental data (Franklin and Miller 2009). SDMs have been used successfully for habitat suitability mapping for resource management and conservation (Carvalho et al. 2010), assessing biological invasions (Robinson et al. 2010), and forecasting future ranges of species (Zimmermann et al. 2009).

SDMs have been criticized because they are correlational models and lack realistic representations of the species' ecology (Guisan et al. 2006, Elith and Leathwick 2009, Hickler et al. 2009). Several studies have responded to these limitations by attempting to incorporate biotic interactions (Gilman et al. 2010), migration limitation (Engler and Guisan 2009), and process-based representations of resource availability (Kearney and Porter 2009, Morin and Thuiller 2009, Buckley et al. 2010).

The environmental datasets used in SDMs are assumed to describe species requirements and limitations at an appropriate spatial scale, or at least are good proxies thereof (Franklin and Miller 2009). However, most studies don't

test the sensitivity of a species to the environmental variables used for building SDMs (Austin 2002, 2007) and spurious projections of such SDMs are reported, e.g. for climatic variables (used in SDMs for plants and birds, Beale et al. 2008, Chapman 2010). An additional criticism of SDMs is that correlational species–environmental relationships are projected onto novel situations assuming a constant relationship between the species and the environmental variables and an unchanging set of constant limitations of the distribution of the species (Elith and Leathwick 2009, Kearney and Porter 2009, Wiens et al. 2009).

Spatial and temporal patterns of soil water availability exert important control over species distributions, and incorporating these patterns into SDMs may represent a substantial improvement beyond traditional bioclimatic models (Austin 2007). Several studies incorporated variables related to water availability with estimates of differing degrees of sophistication. The simplest alternative is to derive variables of water availability directly from climatic variables, such as total annual precipitation or summed monthly differences between potential evapotranspiration and precipitation (Skov and Svenning 2004). Simple soil water models, incorporating some soil information, estimated annual water deficit or related variables with some success (Leathwick et al. 1996, Leathwick and Whitehead 2001, Austin 2002, Guisan et al. 2007). However, Hickler et al. (2009) using LPJ-GUESS, a process-based dynamic global vegetation and vegetation dynamics model (Smith et al. 2001), concluded that although simple indicators of water availability may suffice under current climates, process-based water balance estimates will be needed for future projections. LPJ-GUESS was also used to estimate the water balance in a temperate-humid environment in Europe, which was used in a comparison of climatic and vegetation-based SDMs (Rickebusch et al. 2008), but only two soil layers represented soil water (Smith et al. 2001). Water balance presents a good case study to explore the value of process-based representations in SDMs especially for future climates as they are predicted to become hotter and drier and water availability more limiting (Karl et al. 2009). However, it remains unclear how detailed and how accurate process-based water balance estimates need to be to meet requirements of SDMs, particularly for future projections.

Available soil water is an important link between abiotic and biotic processes that connects climatic conditions with vegetation occurrence. Furthermore, water is one of the most important limiting factors in arid and semiarid regions which cover ca 30% of global land area (Peel et al. 2007). Water availability is a major determinant of net primary production and plant functional composition (Noy-Meir 1973, Sala et al. 1997). For instance, changes in water availability and allocation in a hotter and drier future climate as modeled for a Namibian thornbush savanna could lead to a competitive advantage of shrubs over grasses (Tietjen et al. 2010). Consequently, accurate predictions of future species distributions require precise mapping of soil water availability patterns in space and time, i.e. the ecohydrological niche (Schlaepfer et al. 2011), especially in arid and semiarid ecosystems that are heavily water limited (Loik et al. 2004, Lauenroth and Bradford 2006).

We used sagebrush ecosystems as our test system to compare approaches using a climatic dataset with approaches

integrating detailed soil water availability patterns into SDMs. Sagebrush ecosystems are one of the most widespread semiarid ecosystem types in the western United States and play an important role in the hydrologic cycle of these water-limited regions (McArthur and Plummer 1978, West and Young 2000). They are described as sensitive to the availability of water during summer dry periods in deep soil layers and to the recharge of these deep soil layers, which is most commonly provided by snowmelt in spring or cold-season precipitation (Loik et al. 2004, Williams et al. 2009, Schlaepfer et al. 2011). The shrub *Artemisia tridentata* (big sagebrush) is the most frequent of several *Artemisia* species that are dominants of sagebrush ecosystems. Our analysis focused on ecosystems dominated by *A. tridentata*. These ecosystems represent a crucial habitat for many vulnerable species, including *Centrocercus urophasianus* (greater sage-grouse, Rowland et al. 2006). Livestock grazing and increasingly recreation are the most common land uses. However, land use management, climate change and biological invasions are altering sagebrush ecosystems on a large scale (Bradley 2010).

Our main research objective was to compare SDMs based on climatic datasets with SDMs based on a detailed mechanistic representation of the water balance for a test system sensitive to the patterns and dynamic of available soil water. Our intent was to understand how the addition of process-based information of a relevant ecological resource influences the predictions made by SDMs. We used a high-resolution, multiple soil layer, mechanistic water simulation model to generate a dataset representing water balance of semi-arid ecosystems. Specifically, first we compared the accuracies of current estimates of habitat suitability of sagebrush ecosystems from SDMs based on climatic variables alone with SDMs that are based on a high-resolution simulation of water balance. Second, we compared predictions of SDMs based on the two different datasets for habitat suitability of sagebrush ecosystems under future climate scenarios. When we state that we are interested in the response of sagebrush ecosystems we are not implying that we expect these ecosystems to respond as a unit. Our interests are in the dominant species, big sagebrush, assuming that any ecosystem dominated by big sagebrush, regardless of the exact composition of subordinate species, is a sagebrush ecosystem.

Methods

We focused on the 11 western states of the continental United States, a region containing almost all of the sagebrush ecosystems (Fig. 1a, McArthur and Plummer 1978, West and Young 2000). All spatial data were re-projected to an equal area grid of 10×10 km² using a bilinear interpolation in ArcGIS 9.3.1 (ESRI, CA, USA). The extent of the study area was 3.07×10^6 km², which resulted in 30 705 10×10 km² grid cells.

Sagebrush ecosystem occurrence data

We inferred present potential distribution of sagebrush ecosystems from regional GAP data (grid cells of 30×30 m²) for

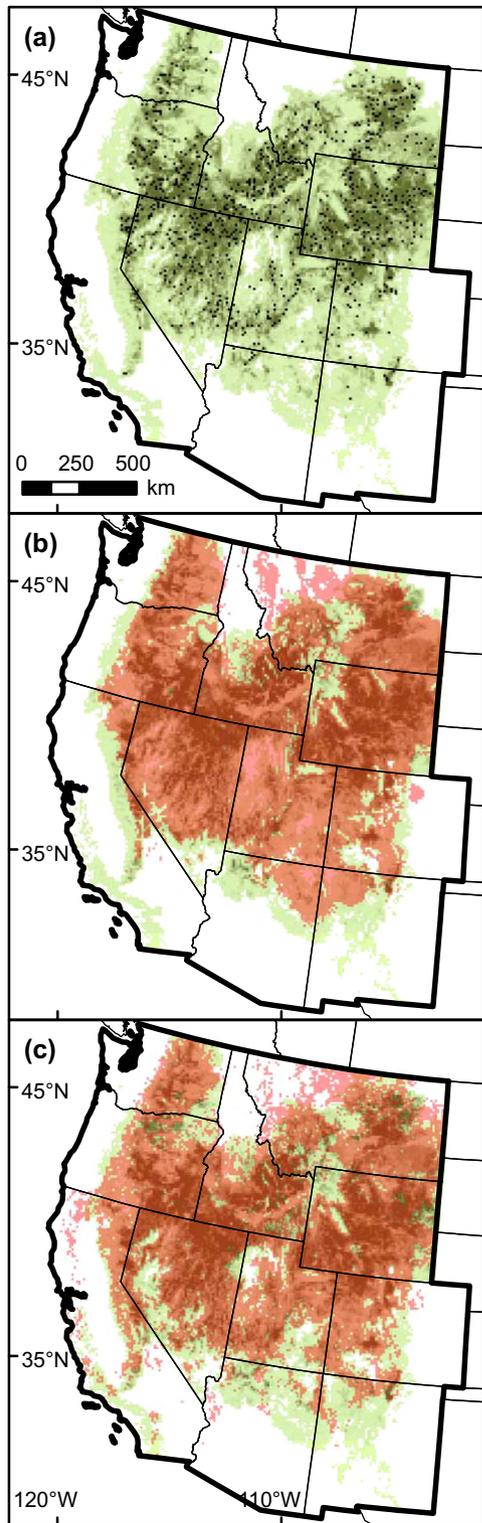


Figure 1. Comparison between observed sagebrush ecosystem extent and estimated sagebrush ecosystem habitat suitability from SDMs. Darker green shades indicate a higher frequency of GAP 30×30 m² grid cells with sagebrush ecosystem occurrence for each re-projected 10×10 km² grid cell in our study area (bold line) of the western US (a). Black cells indicate the 874 random presence sites. Overlay of GAP sagebrush ecosystem distribution and SDMs binary consensus predictions of habitat suitability under current climate conditions (1970–1999, red shaded area) using climatic (b) and ecohydrological datasets (c). These and all following maps have the Albers equal-area conic projection for the contiguous US.

the western US (PNW ReGAP, SW ReGAP, and California, Scott 2007). We included those GAP vegetation types for which *A. tridentata* is a substantial component, i.e. ‘Inter-Mountain Basins Big Sagebrush Steppe’, ‘Inter-Mountain Basins Big Sagebrush Shrubland’, and ‘Inter-Mountain Basins Montane Sagebrush Steppe’ (Schlaepfer et al. 2011). The presence data set was created by randomly sampling 874 10×10 km² grid cells. The probability of a grid cell being selected was directly proportional to the number of 30×30 m² GAP cells of sagebrush ecosystems occurring in the selected cell to reflect the fine-scale distribution of sagebrush ecosystems in the regional GAP data. The non-sagebrush ecosystems cells were used as a pool of absence data (Fig. 1a). For further model validation, we collected an independent dataset of species occurrence based on 1696 unique locations of herbarium specimens (list of accessed herbaria in Supplementary material Appendix 1, Table A1).

Climate scenarios

The climatic dataset included a current climate scenario for which we used the PRISM 800 m average monthly temperature and precipitation data for 1971–2000 (Supplementary material Appendix 1, Table A2, PRISM Climate Group 2008). To represent future climates, we used emission scenario families B1 and A2 for 2070–2099. The B1 scenario has a peak of global population in mid-21st century and rapid changes of the economy towards service and information, whereas A2 describes a world with high population growth and slow technological and economical change (Nakicenovic and Swart 2000). For both future climate scenarios, we used monthly 1/8th-degree downscaled ensemble median temperature and precipitation predictions of 16 global circulation models (accessed May 2010 from <climatewizard.org>, Maurer et al. 2007).

Ecohydrological conditions from soil water modeling

Mechanistic soil water simulation modeling generated the ecohydrological dataset. For every climate scenario and every 10×10 km² grid cell, except those with missing data (e.g. water or rock surface, missing soil data, Fig. 2), we ran SOILWAT, a daily time step, multiple layer, process-based, soil water simulation model, assuming sagebrush vegetation. The model was developed and tested in the semiarid western US shortgrass steppe (Parton 1978, Sala et al. 1992). We adapted it for use in sagebrush ecosystems by incorporating an improved calibrated snow module, the process of hydraulic redistribution, estimations of sagebrush ecosystem-specific vegetation parameters and by testing it against field measured data (Schlaepfer et al. 2011). SOILWAT uses daily weather, monthly vegetation and site-specific properties of each soil layer (lower layer limits: 5, 10, 20, 30, 40, 60, 80, 100, 150 cm, CONUS-SOIL, Miller and White 1998) to simulate the daily ecosystem water balance. This comprises of interception by vegetation and litter, evaporation of intercepted water, infiltration and percolation in the soil profile, bare-soil evaporation, transpiration from each soil layer, and deep drainage (Lauenroth and Bradford 2006, Schlaepfer et al. 2011). Outputs are daily, monthly and annual values of

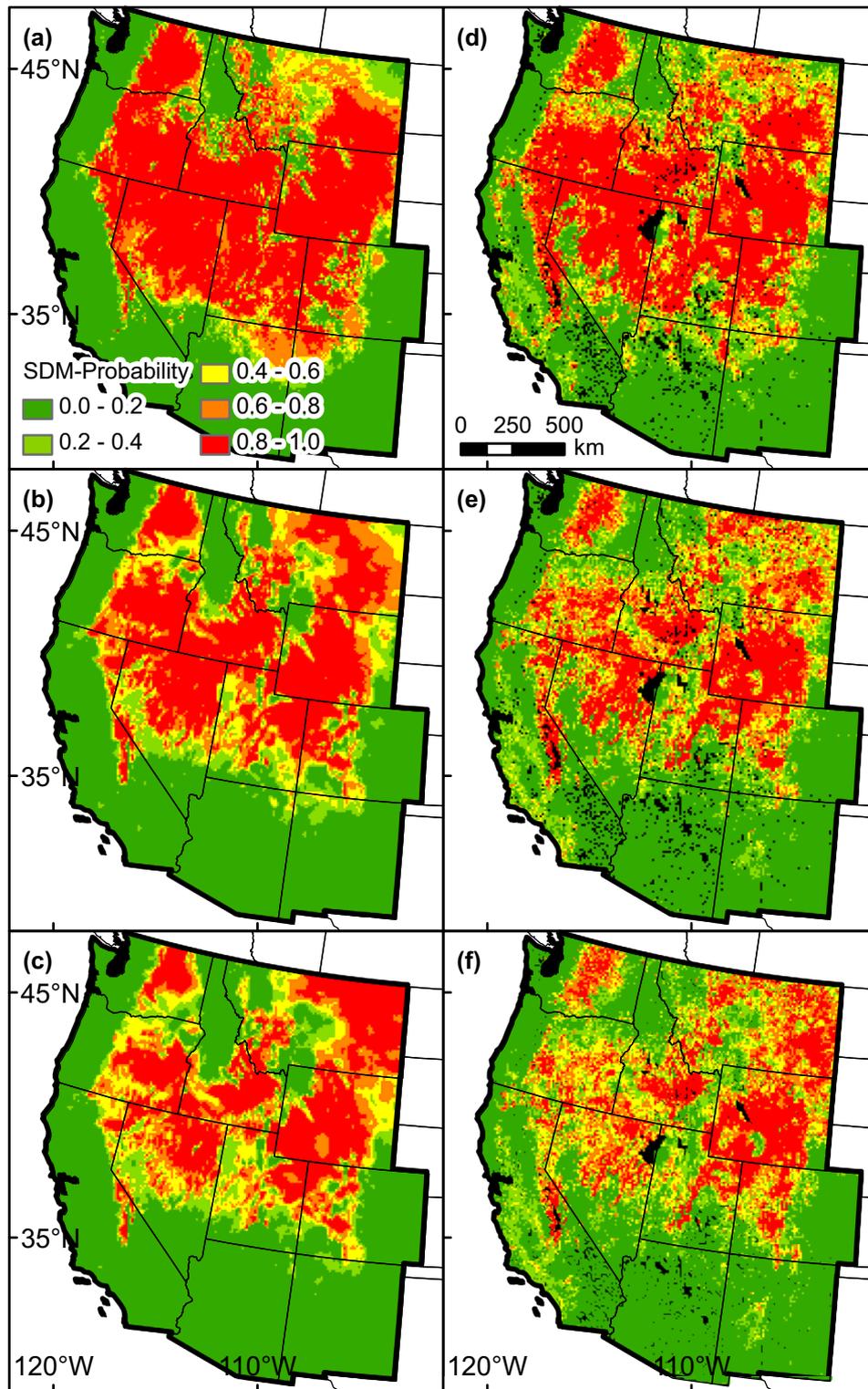


Figure 2. Maps of habitat suitability probabilities indicating predicted sagebrush ecosystem occurrence based on ensemble SDMs using the climatic dataset (a)–(c) and the ecohydrological dataset (d)–(f) under climate scenarios that describe current 1970–1999 (a), (d), future B1 (b), (e), and A2 (c), (f) 2070–2099 conditions in our study area (bold line) of the western US. Black cells indicate data not available.

each water balance component (Parton 1978). To simulate the current ecohydrological conditions, we ran SOILWAT using weather data from 1970–1999 (Maurer et al. 2002). To simulate ecohydrological conditions under climate scenarios B1 and A2, we generated future daily weather from current daily weather conditions by adding predicted average

monthly temperature changes and by multiplying with predicted average monthly precipitation changes for 2070–2099 (see above), thereby maintaining current levels of variability. From the daily SOILWAT output from 30-yr simulations, we derived a dataset (Supplementary material Appendix 1, Table A2), which described sensitive aspects of sagebrush

ecohydrology that are variables describing the overall water balance and the relative contribution of components as well timing, distribution, and seasonality of soil water dynamics and dry periods (Schlaepfer et al. 2011). This ecohydrological dataset was used as input for SDMs.

Sagebrush species distribution modeling

As modeling framework, we calculated ensemble forecasts by combining simulations across sets of initial conditions, model classes, model parameters, and boundary conditions (Araújo and New 2007). We fitted SDMs for nine model classes (generalised linear models, generalised additive models, classification tree analysis, artificial neural networks, surface range envelope, generalised boosting model, Breiman and Cutler's random forest for classification and regression, mixture discriminant analysis, multiple adaptive regression splines) that are combined in the BIOMOD package (Thuiller et al. 2009) for each dataset separately using the random 874 presence sites and an equal number of random absences. Several model classes sample different model parameters, e.g. random forest or artificial neural networks (Araújo and New 2007). To sample different initial conditions, we repeated the analysis ten times drawing random absences from the pool of all absence cells. For each dataset, we retained only those variables that were not highly correlated with another variable (pair-wise correlation coefficients ≤ 0.7 , Supplementary material Appendix 1, Table A2, Leathwick et al. 2005). To sample further different initial conditions, we ten-fold cross-calibrated the models using a random subset of 70% of the data and evaluated them with the remainder of the data and with the herbarium locations as independent data based on the true skills statistics (TSS, Allouche et al. 2006), the area under the curve (AUC) of the receiver operating characteristic (ROC) and Kappa. As alternative measures of accuracy, we also reported sensitivity (proportion of correctly predicted presences) and specificity (proportion of correctly predicted absences, Allouche et al. 2006) with a threshold that maximizes both sensitivity and specificity. We repeated the data splitting for cross-calibration 10 times to evaluate the model and added an 11th final run combining the results. Additionally, we tested the significance of each SDM by comparing the accuracy measures (AUC, Kappa, and TSS) against null distributions of their expected values (Raes and ter Steege 2007). We generated the null-models for each SDM where the presence dataset was randomly allocated to geographic locations. For each draw, we calculated the accuracy measures of the SDM generated from the random presence dataset. We repeated this for 1000 random models and generated a frequency histogram of the accuracy measures. If the accuracy measures of the real SDMs were larger than the values of the 99th percentile of the generated null distribution, then we interpreted this as significance indicating that the accuracy of the SDM is higher than can be expected from a chance relationship between presence of the species and the environmental predictor variables (Raes and ter Steege 2007). To sample different boundary conditions, we then projected potential sagebrush ecosystem distribution with current and future B1 and A2 climate scenarios and based on either the climatic or the ecohydrological datasets. There was a total of 5940 SDMs based on all combinations

of: nine model classes \times three climate scenarios \times two datasets \times ten random absence sets \times eleven cross-calibration steps. Finally, we created six ensemble projections, one for each climate scenario and dataset, by generating probability distributions across model classes and initial conditions (Araújo and New 2007) using TSS as weights for the model classes with a weight decay of 1.6 (Thuiller et al. 2009). We used TSS because of the criticism against AUC (e.g. dependence on spatial model extent, Lobo et al. 2008) and Kappa (unimodal dependence on prevalence, Allouche et al. 2006).

We estimated the importance of the variables by calculating 1 minus the average correlation of the model prediction with predictions based on randomization, repeated 10 times, of the variable in question (Thuiller et al. 2009).

Landscape metrics of simulated sagebrush distribution

We calculated class-level landscape metrics using FragStat v3.3 (McGarigal et al. 2002) for the forecasted distribution of sagebrush ecosystems by the six ensemble projections. We transformed the ensemble projections to binary 'consensus projections' using a threshold that maximizes TSS (Thuiller et al. 2009) and retained only the area for which no data were missing across datasets (mostly due to missing soil data).

Results

Model validation accuracy of both ensemble SDMs was excellent when measured with AUC, while Kappa and TSS indicated an excellent accuracy for the climatic SDM and a good accuracy for the ecohydrological SDM (-1% in AUC, -6% in Kappa and TSS, Table 1). Testing with the independent dataset indicated a lower, but still good, accuracy than cross-calibration, likely due to a biased geographic distribution of herbarium specimens. All tested SDMs had significantly higher model accuracies than expected by chance (Table 2). Accuracy measured by sensitivity and specificity was excellent for both ensemble SDMs with a slight decrease for the ecohydrological SDM (-2% in AUC, -2% in Kappa and TSS, Table 2).

Under current conditions, both ensemble SDMs predicted areas of high suitability for sagebrush ecosystems of similar extent. The predicted areas were matching the GAP input data well, in particular in the central areas of sagebrush ecosystems (Table 3, Fig. 1). Nevertheless, climatic SDMs produced omission errors (1–3%, Table 3) in areas of low sagebrush ecosystem density (as measured by $30 \times 30 \text{ m}^2$ GAP cells per $10 \times 10 \text{ km}^2$ cell) in mountainous areas (Cascades, Sierra Nevada, Coastal Range in southern California, Central Rocky Mountains, Greater Yellowstone Area, central Idaho, and central Montana) and in low to medium density areas at the southern range margin and in northeastern Montana (Fig. 1b). The commission errors (3–4%, Table 3) occurred in northwestern Montana, in several basins (Carson basin, Great Salt Lake and Desert, Canyonlands, and an area of northeastern Arizona and northwestern New Mexico), and in the foothills area of the northern Front Range in Colorado (Fig. 1b). The ecohydrological SDMs produced omission errors (4–5%, Table 3) in low-density areas at the southern range margin and central

Table 1. Validation and accuracy assessments for the climatic and ecohydrological SDM approaches.

Method	Climatic SDM			Ecohydrological SDM		
	AUC ¹	Kappa ^{2,4}	TSS ^{3,4}	AUC ¹	Kappa ^{2,4}	TSS ^{3,4}
Validation based on the average of 10 cross-calibrations	0.99	0.90	0.90	0.97	0.84	0.84
Validation with independent data	0.96	0.81	0.81	0.95	0.75	0.75
Validation of the 11th run with all data	0.99	0.94	0.94	0.99	0.91	0.91
Sensitivity	0.97	0.99	0.98	0.95	0.96	0.96
Specificity	0.97	0.96	0.96	0.95	0.95	0.95

¹AUC values ≥ 0.9 indicate excellent, 0.8–0.9 good, 0.7–0.8 fair, and 0.5–0.7 null to poor prediction accuracy (Thuiller et al. 2009).

²Kappa values ≥ 0.8 indicate excellent, 0.6–0.8 good, and 0.0–0.6 null to fair prediction accuracy (Thuiller et al. 2009).

³TSS values ≥ 0.8 indicate excellent, 0.6–0.8 good, and 0.0–0.6 null to fair prediction accuracy (Allouche et al. 2006).

⁴Kappa and TSS have identical validation values because the prevalence here was equal to 0.5.

Rocky Mountains and in low to medium density areas in the Greater Yellowstone Area, the Black Hill region in Wyoming, in the region of northern Oregon and southern Washington, and partially in northeastern Montana (Fig. 1c). The commission errors (5%, Table 3) occurred in northwestern and northeastern Montana, and in the northern part of the coastal range in California (Fig. 1c). Projections based on climatic SDMs tended to predict more suitable habitats at the southern range, eastern Washington and northern Oregon, and throughout the central areas of sagebrush ecosystems than those based on ecohydrological SDMs (Fig. 1). Ecohydrological SDMs predicted in turn more suitable habitats at range margins in mountainous areas, such as Sierra Nevada, coastal range in California,

Table 2. Significance of SDMs tested by comparing accuracy measures (AUC, Kappa, and TSS) against null-distributions of their expected values based on random models.

SDM method ¹	Accuracy measures at the 99th percentile of null distributions based on 1000 random models			Accuracy measures of the real SDMs ²		
	AUC	Kappa	TSS	AUC	Kappa	TSS
Climatic SDMs						
ANN	0.63	0.20	0.20	0.99	0.93	0.93
CTA	0.89	0.65	0.65	0.99	0.93	0.93
GAM	0.57	0.12	0.12	0.99	0.88	0.88
GBM	0.70	0.31	0.31	0.98	0.86	0.86
GLM	0.57	0.11	0.11	0.98	0.88	0.88
MARS	0.58	0.13	0.13	0.99	0.89	0.89
SRE ³	NA	0.06	0.06	NA	0.72	0.72
Ecohydrological SDMs						
ANN	0.68	0.27	0.27	0.99	0.90	0.90
CTA	0.91	0.69	0.69	0.97	0.88	0.88
GAM	0.59	0.14	0.14	0.97	0.82	0.82
GBM	0.75	0.38	0.38	0.99	0.87	0.87
GLM	0.58	0.12	0.12	0.97	0.82	0.82
MARS	0.61	0.16	0.16	0.97	0.80	0.80
SRE ³	NA	0.06	0.06	NA	0.55	0.55

¹See text for abbreviations of SDM methods. RF and FDA models not included here because RF models produce a constant value of 1 if run on the whole dataset and FDA cannot be run successfully on the whole dataset (Thuiller et al. 2009).

²A SDM performs significantly better than expected by chance alone at a one-sided alpha of 1%, if the model accuracy value is larger than the 99th percentile of the null distribution of 1000 random models.

³There is no AUC associated with SRE models, because these do not calculate probabilities of species occurrence (Thuiller et al. 2009).

Cascades, central Idaho, southern Rocky Mountains, Greater Yellowstone Area, and also northern Montana (Fig. 1). The two ensemble SDMs differed also in the degree of predicted aggregation and fragmentation under current conditions (Table 3). The differences were driven mostly by the number of sagebrush ecosystem patches for which the ecohydrological SDM forecasted a higher number than the climatic SDM which in turn was higher than the value of the GAP input data (Table 3, Fig. 1).

Under future climate scenarios, both ensemble SDMs forecasted small increases and substantial decreases of sagebrush occurrence (Table 3, Fig. 2, 3). Decreases were larger under the A2 scenario than under the B1 scenario (Table 3). The full extent of increases in sagebrush ecosystems could not be evaluated due to study area restrictions. Decreases were more frequently forecasted for southern latitudes and lower elevations, whereas relative increases were mostly indicated for northern latitudes and higher elevations (Fig. 4). Ecohydrological SDMs forecasted a larger decrease throughout the range and this decrease was forecasted not only at the southern range margin as did climatic SDMs. Ecohydrological SDMs predicted also a substantial increase in the number of sagebrush ecosystem patches (B1 vs current prediction, +18%; A2 vs current prediction, +29%), whereas climatic SDMs predicted a decrease (B1, -39%; A2, -30%). The combination of decrease in area and changes in patchiness lead to a strong disaggregation and fragmentation of the distributional range under future conditions based on the ecohydrological SDMs, whereas climatic SDMs prediction didn't change in aggregation and fragmentation increased substantially only under the A2 scenario (Table 3, Fig. 2b–c, e–f).

Variables that strongly influenced climatic SDMs included minimum temperature and different aspects of precipitation (Table 4). Ecohydrological SDMs were driven by variables that describe time and amount of recharge in top soils, actual evapotranspiration, and timing of dry periods in top soils (Table 4).

Discussion

Strength and weaknesses of SDMs based on process-based soil water model variables versus SDMs based on climatic datasets

A model is a generalization of nature that can elucidate the logical consequences of the knowledge and assumptions

Table 3. Measures of change and landscape metrics for the GAP input data and the climatic and ecohydrological SDMs under current climate (1970–1999) and two future climate scenarios (2070–2099).

	GAP input Current	Climatic SDMs			Ecohydrological SDMs		
		Current	B1	A2	Current	B1	A2
Number of sagebrush ecosystem patches	35	56	34	39	168	198	216
Extent of sagebrush ecosystem in western US (%)	62	49	48	36	47	35	33
Predicted change of extent relative to current scenario (%)	NA	NA	-16	-27	NA	-25	-31
Predicted change of extent (90%-confidence interval)	NA	NA	-43 to -9	-52 to -18	NA	-93 to -16	-82 to -21
Predicted increase of extent relative to current (%)	NA	NA	+6	+5	NA	+4	+5
Predicted decrease of extent relative to current (%)	NA	NA	-22	-32	NA	-29	-36
Splitting index ¹	7.9	13	19	28	15	32	37
Aggregation index ²	96	92	93	92	87	81	80

¹The splitting index indicates the effective mesh number of sagebrush ecosystem patches and increases as the patches become more fragmented or increase in number (McGarigal et al. 2002).

²The aggregation index equals 0 when the sagebrush ecosystem is maximally disaggregated and equals 100 when sagebrush ecosystem is maximally aggregated into a single, compact patch (McGarigal et al. 2002).

built into the model, but model predictions are restricted to a domain specified by the built-in relationships (Shugart 1984, Oreskes 2003). Using models to generate projections far into the future, i.e. forecasting impacts of climate change on a species' distribution in 100 yr, are

predictions that cannot be supported or falsified by data that are readily observable. Consequently, such models need to be validated under conditions that are observable and all assumptions used for future projections need to be scrutinized.

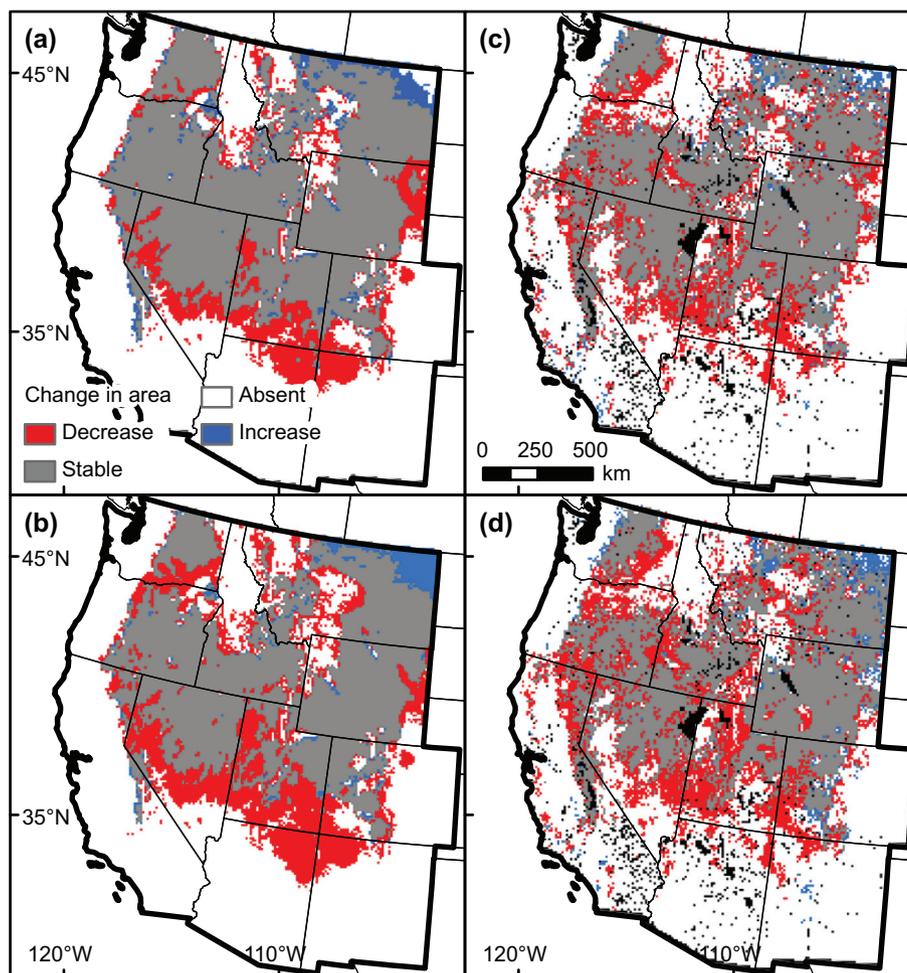


Figure 3. Maps of change in predicted sagebrush ecosystem area based on ensemble SDMs using the climatic dataset (a)–(b) and the ecohydrological dataset (c)–(d) between the current 1970–1999 climate and future B1 (a), (c) and A2 (b), (d) 2070–2099 climate scenarios in our study area (bold line) of the western US. Black cells indicate data not available.

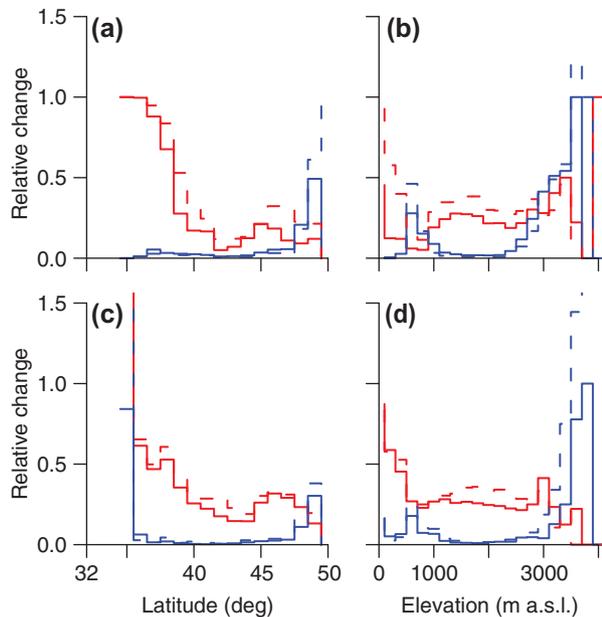


Figure 4. Histograms of relative decrease (red, light lines) and increase (blue, dark) in predicted sagebrush ecosystem area based on ensemble SDMs using the climatic dataset (a)–(b) and the ecohydrological dataset (c)–(d) between the current 1970–1999 climate and future B1 (full lines) and A2 (hashed lines) 2070–2099 climate scenarios for each latitude (a), (c) and 200 m-elevational band (b), (d).

Our study addressed the importance of different datasets for SDMs; we didn't compare SDMs with other model approaches. Specifically, we tested the strengths and weaknesses of a dataset derived from a detailed high-resolution soil water simulation model with a traditional climatic dataset, and compared these with other SDMs based on estimates of water availability of differing sophistication from the literature.

Climatic variables were the first environmental datasets to be used in SDMs; they remain the most commonly used variables in SDMs (Franklin and Miller 2009). They are readily available almost worldwide and provide a direct relationship to assess climate change impacts. Climatic conditions describe patterns of species occurrence (Grinnell 1917). This relationship holds true on at least larger spatial scales (Woodward 1987) because of autocorrelation over large distances of climatic variables (Koenig 2002). However, climatic variables are often only proxies for variables determining species occurrence, e.g. rainfall is a proxy of water availability (Austin 2007). Realized species distributions are restricted by other factors such as dispersal limitations on larger scales and biotic interactions, mostly on smaller scales. Consequently, the strength of the association between climate and species occurrence has been questioned (Beale et al. 2008, Chapman 2010). Nevertheless, here we showed that climatic SDMs for sagebrush ecosystems in semi-arid regions produced accurate predictions under current conditions.

Ecohydrological variables can link climatic proxy variables to estimates of a more mechanistic relationship between environment and species occurrence (Austin 2007). However, ecohydrological variables cannot be measured in situ for entire regions of species distributions; thus, they need to be modeled by soil water simulations. This causes

Table 4. Importance of the variables used for the SDMs based on the climatic and ecohydrological datasets under the present climate scenario.

Variable	Rank	Importance (mean \pm SD)
Climatic dataset		
Mean temperature of the coldest month ($^{\circ}$ C)	1	0.544 \pm 0.060
Summer month precipitation (Jun-Aug; mm)	2	0.331 \pm 0.041
Mean annual precipitation (mm)	3	0.132 \pm 0.020
Normalized mean annual temperature ($^{\circ}$ C)	4	0.041 \pm 0.010
Correlation coefficient between monthly precipitation and temperature	5	0.033 \pm 0.006
Coefficient of variation of monthly precipitation	6	0.033 \pm 0.004
Ecohydrological dataset		
Time of maximum SWP of top soils (month)	1	0.210 \pm 0.029
Actual evapotranspiration (AET, mm)	2	0.146 \pm 0.022
Maximum of ASW in top soils (mm)	3	0.119 \pm 0.020
Start of dry periods of top soils (month)	4	0.102 \pm 0.021
Minimum of available soil water (ASW) in top soils (mm)	5	0.097 \pm 0.012
Correlation coefficient between PET and median SWP of bottom soils	6	0.078 \pm 0.006
Time of maximum soil water potential (SWP) in bottom soils (month)	7	0.055 \pm 0.013
Time of minimum SWP of top soils (month)	8	0.028 \pm 0.004
Ratio transpiration:AET	9	0.025 \pm 0.003
Correlation coefficient between PET and median SWP of top soils	10	0.025 \pm 0.003
Maximum of SWP of bottom soils (MPa)	11	0.014 \pm 0.002
Time of minimum SWP of bottom soils (month)	12	0.012 \pm 0.003
Minimum of SWP of bottom soils (MPa)	13	0.009 \pm 0.003
Start of dry periods of bottom soils (month)	14	0.007 \pm 0.002

potential caveats: 1) a new model brings new assumptions, 2) additional data are needed, e.g. soil and vegetation parameters, and 3) the spatial resolution of soil water models and SDMs should match. First, the soil water simulation model SOILWAT represents mechanistically the relevant water balance components of semi-arid ecosystems (Parton 1978, Sala et al. 1992) and produces realistic high-resolution water budgets for sagebrush ecosystems (Schlaepfer et al. 2011). Therefore, we assumed that ecohydrological variables estimated by SOILWAT appropriately represented the causal relationships between water availability and sagebrush ecosystems occurrence. Second, SOILWAT simulations were based on a simple vegetation model for an average sagebrush ecosystem based on literature estimates for monthly vegetation parameters (Schlaepfer et al. 2011). Soils were represented by the best data available, i.e. 1-km² gridded STATSGO data with several areas of missing data (CONUS-SOIL, Miller and White 1998). STATSGO is based on generalized map units composited of associated soil series with a minimum spatial resolution of ca 6 km² that leads to uncertainties in spatial and depth parameter estimates (Miller and White 1998). Third, the spatial heterogeneity of soil processes is inherently much higher than that of climatic variables.

However, to ensure spatial comparability among climatic and ecohydrological datasets, we aggregated all data to the same spatial resolution which reduced information on soil heterogeneity. Spatial resolution influences the reliability of species occurrence data, particularly when the heterogeneous environmental conditions experienced by the species within the cells may not match well the aggregated environmental factors across cells (Skov and Svenning 2004, Franklin and Miller 2009). Nevertheless, the ecohydrological dataset reduced model accuracy and performance under current conditions slightly (−1% in AUC, −4% in Kappa and TSS). Additionally, it predicted a too high number of patches compared to GAP input data. Our results apparently contradict theoretical expectations (Austin 2002, 2007) and earlier attempts incorporating mechanistic water balance representations into SDMs (Rickebusch et al. 2008).

Outlook on the use of SDMs

There are several possible, mutually non-exclusive explanations for the slightly poorer performance of our ecohydrological SDMs of sagebrush ecosystems, which may suggest approaches to further improve SDMs in general. First, semi-arid systems are overwhelmingly driven by water limitations; for instance, actual evapotranspiration approximates mean annual precipitation (Lauenroth and Bradford 2006). Therefore, climatic variables dominate ecosystems and hence may adequately predict patterns of water availability well enough for successful distribution modeling. Second, occurrence of sagebrush ecosystems is not determined exclusively by ecohydrological factors, even though they are important drivers, thus the SDMs based on the ecohydrological dataset performed slightly worse. Therefore, it appears promising to investigate a dataset combining climatic and ecohydrological variables to which sagebrush ecosystems are sensitive. For instance, our results and an earlier study using SDMs for big sagebrush (Shafer et al. 2001) suggest minimum temperature has a limiting physiological function (as shown in combination with drought stress for big sagebrush seedlings, Lambrecht et al. 2007). Third, on the gradient of sophistication of water balance estimates used in SDMs, our approach is at the higher end focusing on high-resolution soil information, but not incorporating detailed vegetation dynamics such as in the use of LPJ-GUESS (Rickebusch et al. 2008). We may have hit an ‘intermediate-sophistication depression’ where simpler models represent transformed climatic variables and more complicated models incorporating vegetation dynamics represent necessary details we omitted here. Fourth, our accuracy measures may be incorrect because they are based on a comparison with the GAP vegetation data directly. The GAP data themselves are only model results of vegetation types and are not directly presence data of a species. We also pooled presence data across sagebrush ecosystems dominated by big sagebrush; however, big sagebrush shows considerable ecological and genetic variation at subspecies level (McArthur and Sanderson 1999) which could have led the SDMs astray. Further, we compared model predictions against an aggregated GAP dataset with 10×10 km² cells showing presence if only one of the 30×30 m² sub-cells indicated sagebrush ecosystems. Through our random

sampling scheme, cells with a higher density of sagebrush ecosystems sub-cells were selected with a higher probability which lead to an under-representation of low density areas. Accordingly, many omission errors occurred in low-density areas. However, if we superimposed a density threshold on the GAP data, the distribution becomes much patchier and starts to be better described by predictions of the ecohydrological SDMs.

Future potential distribution of sagebrush ecosystems

Our SDMs incorporated several levels of uncertainty for forecasts of ecosystems dominated by big sagebrush occurrence. The first is variation caused by model classes, which was accounted by averaging across nine SDM techniques that were tested against expectations under random processes, and variation caused by different initial conditions, which was incorporated by multiple random sampling of absence data and by cross-validation. The second is uncertainty about future climatic conditions, which was taken into account by running SDMs for two contrasting climate change scenarios, each driven by consensus results from 16 GCMs. Because of the small sample of boundary conditions, our ensemble forecasts depend upon the median climate forecasts in those scenarios (Araújo and New 2007) and should be taken as indicative rather than predictive of the possible future states of sagebrush ecosystem.

Even though ecohydrological SDMs performed slightly poorer than climatic SDMs in this study, their accuracy was still good and overall current predictions were comparable. A general geographic pattern of future sagebrush occurrence emerged from our analysis and is characterized by substantial decreases in the southern part of the range and increases in the northern parts corroborating earlier results (Shafer et al. 2001, Bradley 2010). Our SDMs also forecasted small increases at higher elevations, e.g. at the interface with coniferous forest. These areas of predicted change are candidates for monitoring early signs of sagebrush ecosystem responses to climate change.

Several factors influence sagebrush ecosystem distribution. Shafer et al. (2001) inferred that the simulated northward shift in sagebrush was a response to increased minimum temperature. They also suggested that a combination of increased transpiration in winter and changes in the precipitation regime may lead to drier soils during the summer and to increased fire frequency which both result in decreases of *A. tridentata* (Shafer et al. 2001). Bradley (2010) found a large-scale contraction of suitable habitat due to changes in summer precipitation and temperature. Our results from the climatic SDMs confirmed that minimum temperature and precipitation regime are important factors determining present and future occurrence of sagebrush ecosystems. Greatest increases in minimum temperature are predicted for the central and northeastern parts of the region, whereas greatest decreases in summer precipitation are predicted for the northwestern part (Karl et al. 2009). Our results from the ecohydrological SDMs can provide a mechanistic interpretation for those changes by transforming climatic factors into ecosystem-relevant variables, i.e. the amount of available soil

water, timing of recharge of different soil layers, and seasonality of soil water.

Important differences in the projected future suitable habitat of sagebrush ecosystems were evident between ecohydrological SDMs and climatic SDMs in magnitude of decrease and in patchiness and disaggregation at small and large spatial scales. Although the patchiness predicted by ecohydrological SDMs was already elevated under current conditions, the number of patches increased considerably under future climates whereas climatic SDMs suggested instead a decrease at roughly comparable predicted spatial extents of suitable habitat. The forecasts, particularly from the ecohydrological SDMs, suggest potential large spatial scale splitting of sagebrush ecosystems into several disjunct areas, i.e. Washington, Sierra Nevada area, areas in Oregon and northern Nevada, central Idaho, and an area in eastern Utah, Wyoming, Colorado, and eastern Montana (Fig. 3, 4). Climatic SDMs forecast splitting into fewer, larger areas. These different forecasts for future habitat suitability of sagebrush ecosystems have important consequences because patchiness, size of patches, and fragmentation are important factors influencing genetic structure and dynamics of populations and communities (Loveless and Hamrick 1984, Kareiva et al. 1990). For instance, sagebrush obligate species, such as greater sage-grouse, require large patches of sagebrush ecosystem as habitat (Rowland et al. 2006). Furthermore, total number of species associated with sagebrush ecosystems is expected to decrease within each of the patches with decreasing area (He and Hubbell 2011). For big sagebrush itself, the splitting of its range into disjunct patches, could bear important genetic consequences. Big sagebrush is taxonomically divided into several subspecies with diverging ecological occurrence and physiological adaptations (Kolb and Sperry 1999, McArthur and Sanderson 1999, Lambrecht et al. 2007). Genetic distance among big sagebrush taxa could increase because of decreased genetic exchange among individuals from disjunct patches. Additionally, climate change may alter forces of natural selection, which could lead to further ecological divergence of big sagebrush in different disjunct patches. Moreover, these consequences are exacerbated by other components of global change, such as land use and invasive species that further reduce suitable habitat and increase disaggregation of sagebrush ecosystems (Bradley 2010). We are in need of a deeper understanding of what the differences between SDMs based on different datasets, e.g. climatic and ecohydrological datasets, both valid, good, and reasonable approaches, signify to improve our insight of the precise trajectories and mechanisms of future change in species distribution.

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Supplementary material (Appendix E6928 at <www.oikosoffice.lu.se/appendix>). Appendix 1.