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Ecological niche model comparison under different climate scenarios: a case study of *Olea* spp. in Asia

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Abstract. Ecological niche modeling (and the related species distribution modeling) has been used as a tool with which to assess potential impacts of climate change processes on geographic distributions of species. However, the factors introducing variation into niche modeling outcomes are not well understood: To this end, we used seven algorithms to develop models (Maxent, GARP, BIOCLIM, artificial neural networks, support-vector machines, climate envelope, and environmental distance) to estimate the potential geographic distribution of olives (*Olea europaea* sensu lato, including *Olea ferruginea*) under two climatic data sets (current 2000 and future 2050). Five general circulation models and two representative concentration pathway scenarios were used as predictor variables in future projections of the geographic potential of this species; models were fit at global extents (10′ spatial resolution) but transferred and interpreted for a region of particular interest in Central Asia, which largely avoids problems with truncation of niche estimates. We found marked differences among approaches in predicted distributions and model performance, as well as in the future distributional pattern reconstructed, from one algorithm to another. These general approaches, when model-to-model variation is managed appropriately, appear promising in predicting the potential geographic distribution of *O. europaea* sensu lato and thus can be an effective tool in restoration and conservation planning for wild populations, as well as possible commercial plantations of this species.

Key words: climate change; ecological niche model; invasive species; partial receiver-operating characteristic (ROC); species distribution model.

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Introduction

Climate change has affected the weather patterns of the Earth radically. Effects of climate change on biological species can be estimated by comparing temperature and precipitation patterns and trends in relation to species' distributional shifts (Peterson et al. 2015). Climate change also may deplete and rearrange distributions of plant and animal species that contribute to the functioning of natural ecosystems and the services that they provide (Tallis et al. 2008). Future climate patterns will likely have strong impacts on species' geographic distributions (Garcia et al. 2014), with the general expectation that species' distributions will shift poleward and upward in elevation (Hickling et al. 2006).

Ecological niche modeling (and the related species distribution modeling) represents an effort to estimate dimensions of the fundamental ecological niche, and therefore, it can predict the probability of environmental suitability for a species in an area (Cardona and Loyola 2008, Peterson et al. 2011); numerous modeling algorithms have been developed to meet these challenges (Elith et al. 2006). The complexity of natural systems necessitates diverse modeling approaches (Carpenter et al. 1993, Stockwell 1999, Hirzel et al. 2002, Pearson et al. 2002, Thuiller 2003, Elith et al. 2006, 2010, Phillips et al. 2006, Elith and Leathwick 2007, 2009), and no single approach is likely to be the best in all cases (Qiao et al. 2015). In geographic space, these methods identify the potential distribution of a species over the full set of grid cells, which are the cells that are most similar (in some sense, depending on the algorithm) to cells that are known to be occupied by the species (Negga 2007, Kgosiesele 2010, Cunze and Tackenberg 2015).

We used as a case study and worked example the tree species *Olea europaea* sensu lato: *Olea* grow as woody vines, shrubs, and trees (Nasir and Rafiq 1995) and are common in dry, moist temperate, and sub-tropical regions of the world. *Olea europaea* sensu lato occurs in regions with 800–1200 mm rainfall and annual mean temperatures of 14–18°C (Hines and Karlyn 1993). In Central Asia, this species ranges up to 2400 m in elevation (Joshi 2012). Olives also occur in New Zealand, South Africa, and along the coastal areas of Australia, Europe, and China (International Olive Council 2013).

Olea europaea sensu lato is an evergreen species that has many uses. Their fruit is used for food (olives), and the plant also has medicinal uses. The leaves and fruit contain polyphenols and antioxidants that are used to treat health problems as an antitumour, anti-inflammatory, antioxidant, antipruritic, antiallergic, immunomodulatory, and antiviral agents. Their roots are beneficial in treating scorpion stings, asthma, rheumatism, and headache (Joshi 2012). Factors such as phenotypic plasticity, functional traits, and genetic effects have also been studied by a number of researchers (Wang et al. 2010, Benito Garzón et al. 2011, Stahl et al. 2014, Valladares et al. 2014).

Numerous approaches are available for estimating species' ecological niches and predicting their potential geographic distributions (Guisan and Zimmermann 2000). Many comparative evaluations have been developed among multiple approaches (e.g., Elith et al. 2006), but fewer evaluations have assessed model transfers in a comparative sense (e.g., Pearson et al. 2006). Certainly, model transfers are complicated by the limited representation of environments across regions over which models are calibrated (Saupe et al. 2012, Owens et al. 2013), which led to the concept of the existing niche, defined as the part of the fundamental ecological niche that is actually represented over relevant areas (Peterson et al. 2011). Here, we take advantage of the global nature of the distribution of *Olea europea* sensu lato to calibrate more comprehensive ("Hutchinsonian," in the sense of Saupe et al. 2012) models than is possible in any more limited region. Our main objective was to compare results of seven approaches to estimating ecological niches of species (Maximum Entropy [Maxent], genetic algorithm for rule-set prediction [GARP], BIOCLIM, artificial neural networks [ANN], support-vector machines [SVM], climate space [CE], and environmental distance [ED]), and to evaluate their consistency and variation in predicting the potential distribution of *Olea europea* in Central and South Asia under current and future climate scenarios (Representative Concentration Pathway; RCP 4.5 and RCP 8.5).

Methods

Study area and input data

Given the near-global distribution of *Olea europea* sensu lato, either as a native species or as an introduced species, we had the opportunity to calibrate models across broad and diverse landscapes. Calibrating models across the most extensive areas possible allows assessment of the niche dimensions of the species across the most diverse environmental background possible, which helps greatly to avoid problems with truncation of representation of environments and associated model extrapolation (Owens et al. 2013). As such, our model calibration area was the entire world (minus Antarctica and oceanic areas). However, the region of particular interest in our analysis was Central and South Asia (5.68–53.93° E, 37.58–102.40° N), with adjoining areas of North Africa and the Arabian Peninsula. The global extent for model calibration was chosen in consideration of the accessible area (**M**) of the species (Barve et al. 2011), whereas the Asian focus of interpretation was based on the motivations of this study and the region of origin of most of the authors.

Primary occurrence data (Fig. 1) with geographic coordinates were extracted from the literature (Ahmed et al. 2009, Ashraf et al. 2016) and from the Global Biodiversity Information Facility (www.gbif.org). A gap in the distributional data centered on Pakistan was filled by on-ground surveys. In all, 33,647 points were gathered for the occurrence of the species worldwide, but showed notable clusters and clumping; we used SDMTools (Brown 2014) to rarefy these points spatially such that no pair of points was closer than 10 km; this step left 3557 points for model calibration. Species distribution data were separated evenly into calibration and evaluation subsets at random to permit rigorous model evaluation.

To permit model transfers into the future, we focused model calibration on climatic variables, which center on temperature and precipitation as important drivers of distributions of species. Environmental variable selection depends on their impacts on the distributional potential of the species; considerable collective experience points to a significant role for climate in this regard (Pearson 2007, Kumar and Stohlgren 2009). We obtained 19 so-called bioclimatic variables from the WorldClim archive (Hijmans et al. 2005, http://www.worldclim.org/) at spatial resolutions of 10′ (global extents, for model calibration) and 2.5′ (Asian area of interest, for model transfer). For the assessment of future distributional potential, we downloaded corresponding data layers from the CCAFS (Climate Change, Agriculture and Food Security)-downscaled general circulation model (GCM) data portal (http://www.ccafs-climate.org/), in the form of data for two emissions scenarios (RCP 4.5 and RCP 8.5) and five GCMs: MIROC-MIROC 5, NCAR-CCSM 4, MOHC_HADGEM 2.CC, MPI-ESM-MR, and GISS-E2-R-CC. We downloaded future climate data at 2.5′ spatial resolution for both RCP scenarios.

Data processing

Our general plan of analysis was to calibrate and evaluate models at global extents at 10′

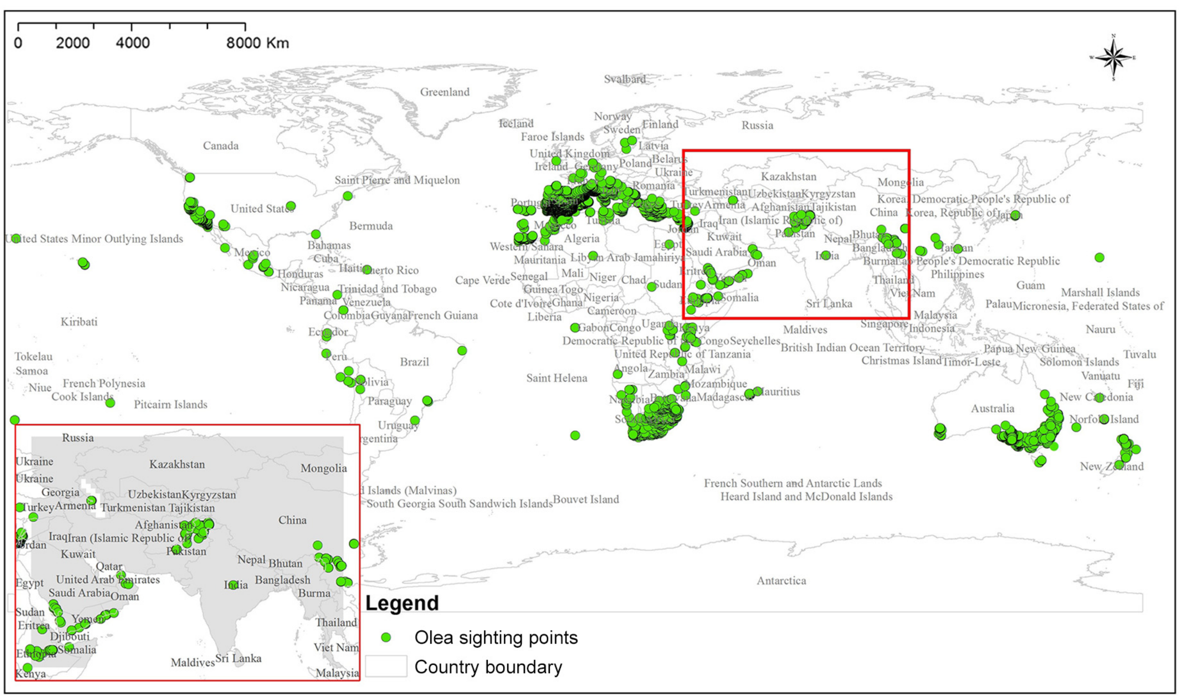

Fig. 1. Current distribution of *Olea europaea* sensu lato worldwide.

spatial resolution and then transfer them to the Asian study area at 2.5′ resolution for exploration and assessment, as is summarized in Fig. 2. One approach (Maxent) was implemented in a standalone software platform (https://www.cs.princeton.edu/~schapire/maxent/); the remaining approaches were run via the openModeller platform, which is designed to facilitate comparative analyses (de Souza Muñoz et al. 2011). We evaluated all present-day climate variables (10′, global extent) for highly correlated variables using SDMTools: One variable was removed from any pair of variables showing Pearson's product–moment correlations >0.9 (Table 1).

Diverse approaches are available for modeling; here, we focused on Maxent (Phillips et al. 2006), GARP (Stockwell 1999), BIOCLIM (Nix 1986), ANN (Pearson et al. 2002), and SVM (Drake et al. 2006); we also used the CE and ED implementations within openModeller. We used Maxent version 3.4.0k, available from at http://www.cs.princeton.edu/~schapire/Maxent/ (Phillips et al. 2017). We chose the random seed and 10 bootstrap replicates options, and left the remaining parameters at default values.

For the remaining approaches, we used openModeller version 1.1.0 (Giannini et al. 2010), available from http://openmodeller.sourceforge.net/. openModeller is a platform that hosts multiple algorithms that can be implemented in parallel under comparable circumstances. We used the GARP "best subsets-openModeller" implementation, plus BIOCLIM, ANN, SVM, CE, and ED. In each case, we calibrated models globally (10′) for current conditions, and transferred models to the Asian region (2.5′) for interpretation. We evaluated

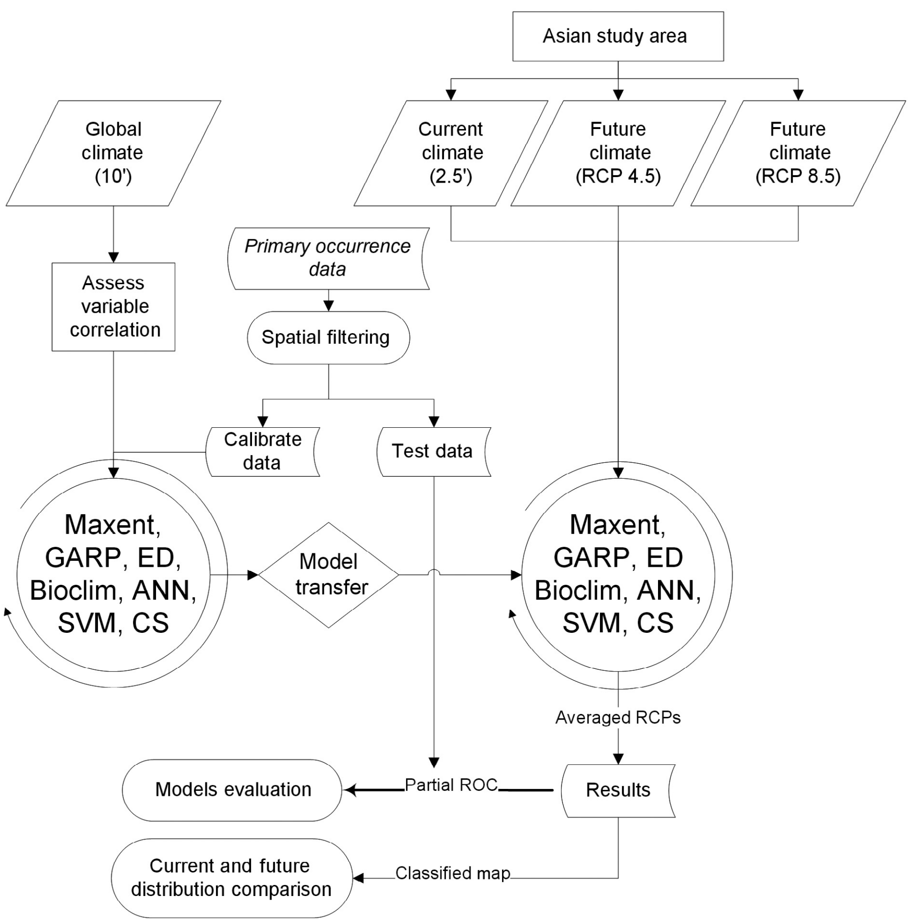

Fig. 2. Flowchart summary of data processing steps in this study.

Table 1. Pearson's product-moment correlations among the 15 original "bioclimatic" variables.

Bio	1	2	3	4	5	6	7	10	11	12	13	14	15	16	17
1															
2	0.5														
3	0.8	0.3													
4	−0.8	−0.2	−0.8												
5	0.9	0.7	0.6	−0.5											
6	**0.9**	0.3	0.8	−0.9	0.7										
7	−0.7	0.0	−0.8	**0.9**	−0.3	−0.8									
10	**0.9**	0.6	0.6	−0.5	**0.9**	0.8	−0.4								
11	**0.9**	0.4	0.8	−0.9	0.8	**1.0**	−0.8	0.8							
12	0.3	−0.2	0.5	−0.5	0.1	0.4	−0.6	0.2	0.4						
13	0.4	−0.1	0.5	−0.5	0.2	0.5	−0.5	0.3	0.5	0.9					
14	0.0	−0.3	0.2	−0.2	−0.1	0.1	−0.3	−0.0	0.1	0.7	0.3				
15	0.3	0.5	0.2	−0.1	0.4	0.2	−0.0	0.4	0.3	−0.1	0.1	−0.5			
16	0.4	−0.1	0.5	−0.5	0.2	0.5	−0.5	0.2	0.5	**0.9**	**0.9**	0.4	0.0		
17	0.0	−0.3	0.2	−0.2	−0.1	0.2	−0.3	−0.0	0.1	0.7	0.4	**0.9**	−0.5	0.4	

Notes: Correlations above $r = 0.9$ are shown in boldface. Variables 8, 9, 18, and 19 were omitted owing to known spatial artifacts.

model predictions using the evaluation data subset at global extents. We averaged across all individual GCM predictions separately for RCP 4.5 and 8.5 to provide a best guess as to the species' response under two scenarios of future climate.

An important first step in assessing the outputs of a study such as this one is a formal statistical test to establish whether models are able to predict independent subsets of occurrence data better than random expectations. The commonly used true skill statistics and Cohen's kappa both require absence data, as well as presence data, and so are not applicable in situations such as this one. We used partial receiver-operating characteristic (ROC) approaches, as they avoid at least some of the failings of classical ROC approaches (Peterson et al. 2008). We used an acceptable omission error threshold of $E = 10$ (introduced in Peterson et al. 2008), and 1000 replicate 50% bootstrap resamplings to establish whether the ROC AUC (area under the curve) ratio was above 1.0. Partial ROCs were computed using online tools at http://shiny.conabio.gob.mx:3838/nichetoolb2/. Significance of partial ROCs was assessed by direct count of the proportion of replicate analyses with an AUC ratio ≤1.0.

We simplified model outputs and improved comparability among modeling approaches by means of omission error-scaled thresholding. That is, we began with lowest training presence areas: the highest suitability level that includes 100% of the data on which the model was calibrated ("T_{100}"; Pearson et al. 2007). When error may exist among the available data, it is useful to reduce the percentage included by the acceptable omission rate E (Peterson et al. 2008); hence, we explored $T_{100\text{-}E}$ for $E = 5\%$ and $E = 10\%$, such that higher acceptable omission rate values identify smaller areas and higher confidence in suitability.

Results and Discussion

Model performance

Initial assessments of correlations between environmental variables indicated four pairs of variables with Pearson's correlation coefficients >0.9 (Table 1); removing variables from the environmental dataset to avoid these correlations, we ended up with mean diurnal range, isothermality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, annual precipitation, precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality as environmental dimensions for modeling. Minimum temperature of the coldest month and maximum temperature of the warmest month were the most informative variables for *Olea europaea* sensu lato; these variables were the top two predictors in the Maxent model. The least important variables were precipitation of the driest month and precipitation seasonality. Model outputs in terms of global extents were all roughly comparable, corresponding more or less closely to the known occurrences of the species. Table 2 summarizes the results of the partial ROC analyses: Results from all approaches except CS had all replicate AUC ratios >1, such that Maxent, GARP, BIOCLIM, ANN, SVM, and ED models yielded predictions that were significantly better than random expectations ($P <$ 0.001). For CS, however, none of the replicate AUC ratios was >1, so we conclude that its predictions were not better than random expectations (Table 2; Appendix S1: Figs. S1–S7).

Phillips et al. (2006) found that GARP and BIOCLIM overpredicted suitable areas for plant and animal species. Tarkesh and Jetschke (2012) found that Maxent performed better than BIOCLIM and GARP. Márquez (2006) compared models for two herpetofaunal species at different scales, and again concluded that Maxent offers better predictions compared to BIOCLIM and GARP. However, other authors have pointed out that the metric of performance can have serious effects on these conclusions and that average performance does not inform particularly effectively regarding model performance in any particular case (Qiao et al. 2015). A general summary of our results, then, specifically as regards successful prediction of the random subset of the available occurrence data, is that the best of the approaches was Maxent, followed by GARP, SVM, BIOCLIM, and ANN.

Current and future distributional potential

Model results were developed for two RCP emissions scenarios for future climate conditions across Central and South Asia. Thresholded maps showed clearly the differences between results obtained by different approaches, both in the present (Fig. 3) and under future conditions (RCP 4.5 and RCP 8.5; Figs. 4 and 5). Maxent models for the present day covered 5.9% of the total study area under a T_{10} assumption set; transferring these models to future conditions yields predictions that covered 1.2 and 1.1% of the Asian study area for RCP 4.5 and RCP 8.5, respectively (Table 3, Figs. 4 and 5). This prediction covered parts of southeastern China, Himalayan Burma and on the Potohar Plateau, and parts of Afghanistan, Turkmenistan, Armenia, Yemen, and Somalia (Figs. 4 and 5).

Genetic algorithm for rule-set prediction anticipated a somewhat broader potential area for the species, covering 5.0% of the Asian study area in the present (Fig. 3) and 4.8 and 4.7% of the area

Table 2. Summary of partial ROC values and AUC ratios for seven approaches to estimating the ecological niche of *Olea europea* sensu lato.

	Maxent	GARP	Bioclim	ANN	SVM	CE	ED
AUC at 0.1							
Minimum	0.528	0.512	0.744	0.759	0.541	0.425	0.653
Maximum	0.589	0.580	0.839	0.865	0.607	0.462	0.706
Average	0.559	0.540	0.794	0.817	0.573	0.442	0.676
SD	0.010	0.010	0.014	0.019	0.011	0.005	0.008
AUC at 0.5							
Minimum	0.496	0.485	0.500	0.500	0.494	0.474	0.495
Maximum	0.499	0.495	0.500	0.500	0.497	0.488	0.499
Average	0.498	0.490	0.500	0.500	0.495	0.481	0.497
SD	0.000	0.002	0.000	0.000	0.000	0.002	0.000
AUC ratio							
Minimum	1.061	1.049	1.488	1.519	1.091	0.896	1.315
Maximum	1.182	1.174	1.677	1.731	1.224	0.948	1.416
Average	1.124	1.100	1.588	1.634	1.156	0.920	1.358
SD	0.020	0.018	0.028	0.038	0.021	0.007	0.015
Probability	<0.001	<0.001	<0.001	<0.001	<0.001	>0.001	<0.001

Note: ANN, artificial neural networks; CE, climate space; ED, environmental distance; GARP, Genetic algorithm for rule-set prediction; ROC, receiver-operating characteristic; SVM, support-vector machines.

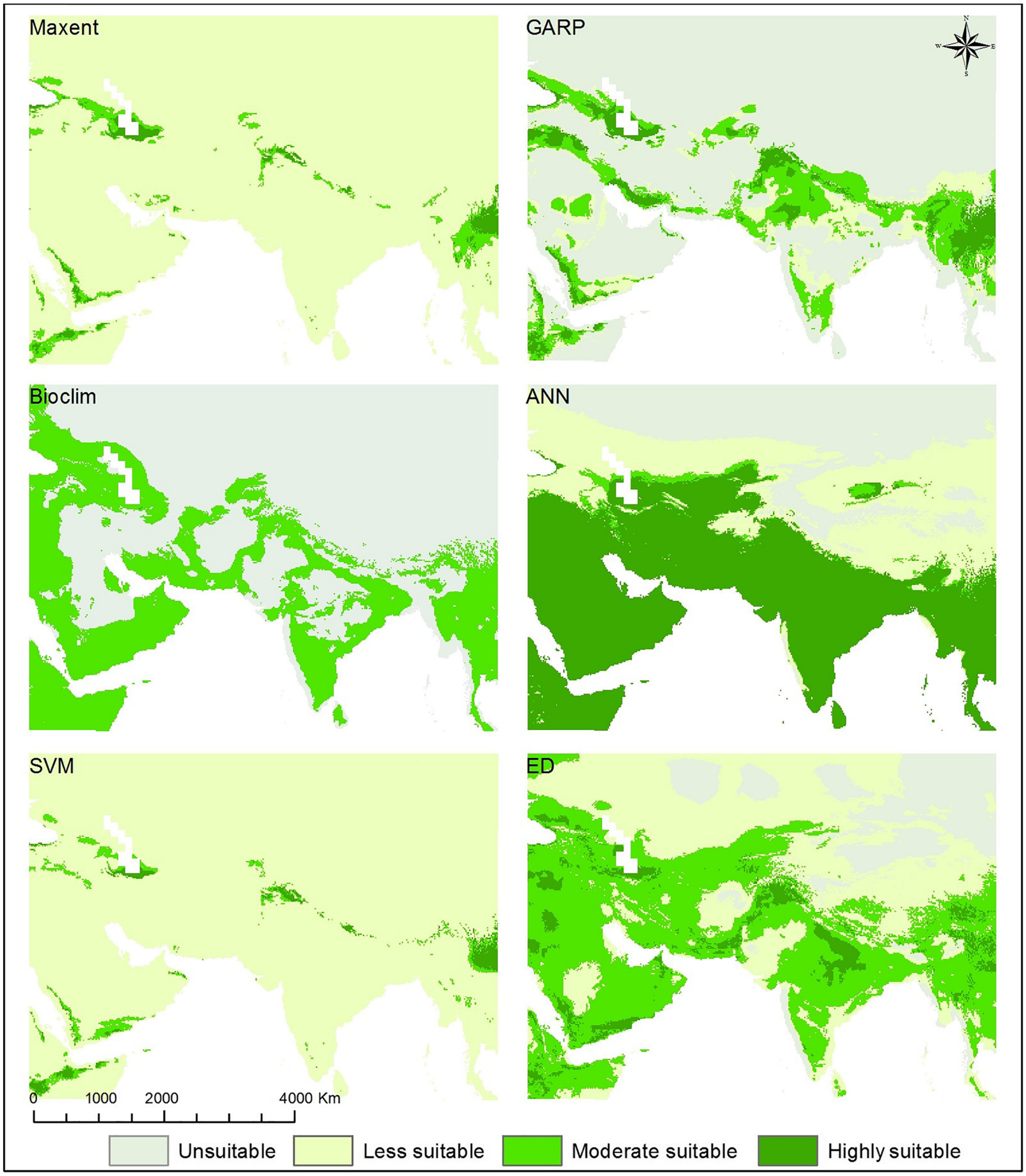

Fig. 3. Comparison of classified maps of seven approaches to modeling the ecological niche of *Olea europaea* sensu lato for present-day climate conditions across Central and South Asia projection at 2.5′ spatial resolution.

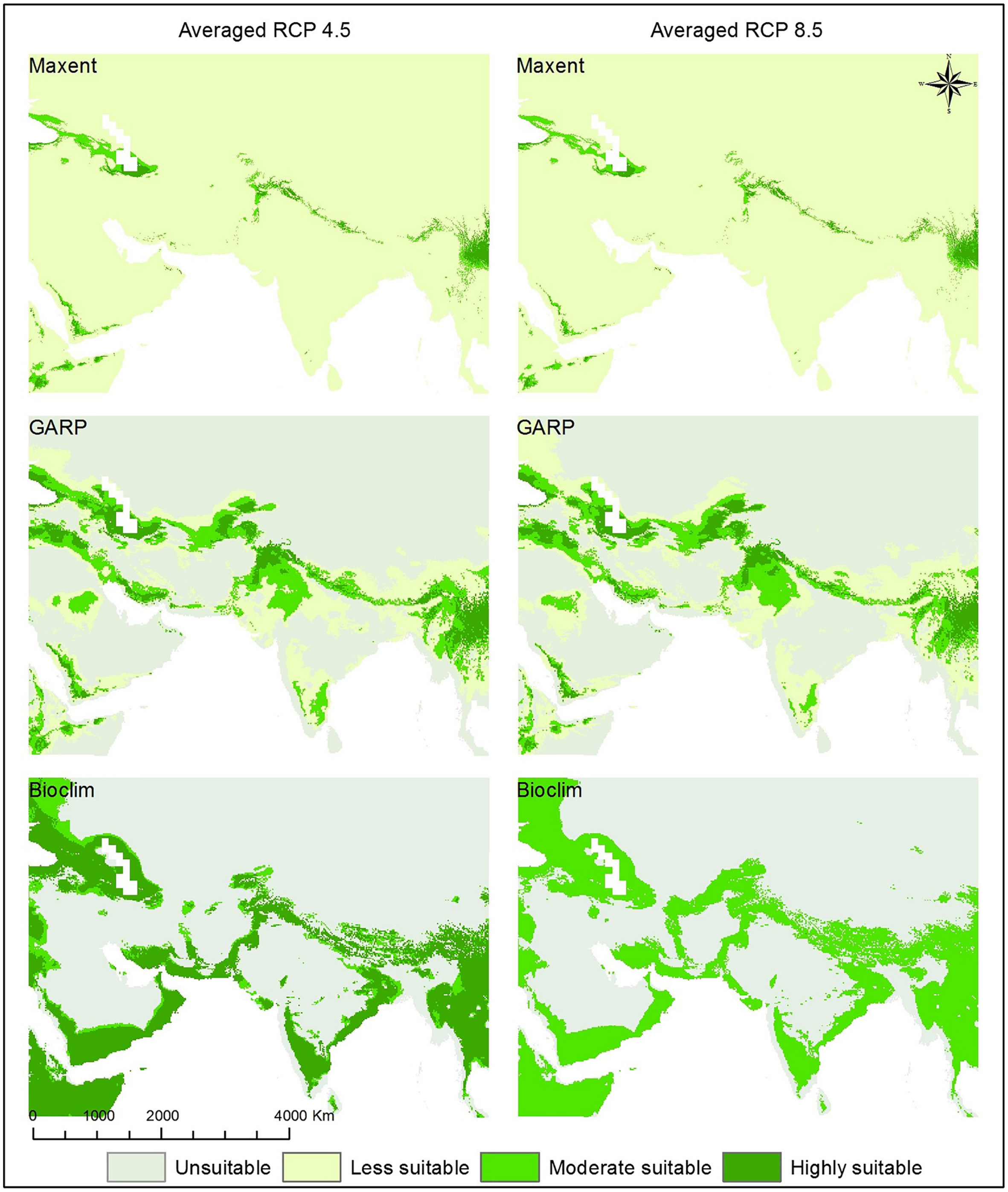

Fig. 4. Maps of modeled future potential distribution for *Olea europaea* sensu lato from Maxent, genetic algorithm for rule-set prediction (GARP), and BIOCLIM (left side: RCP 4.5; right side: RCP 8.5).

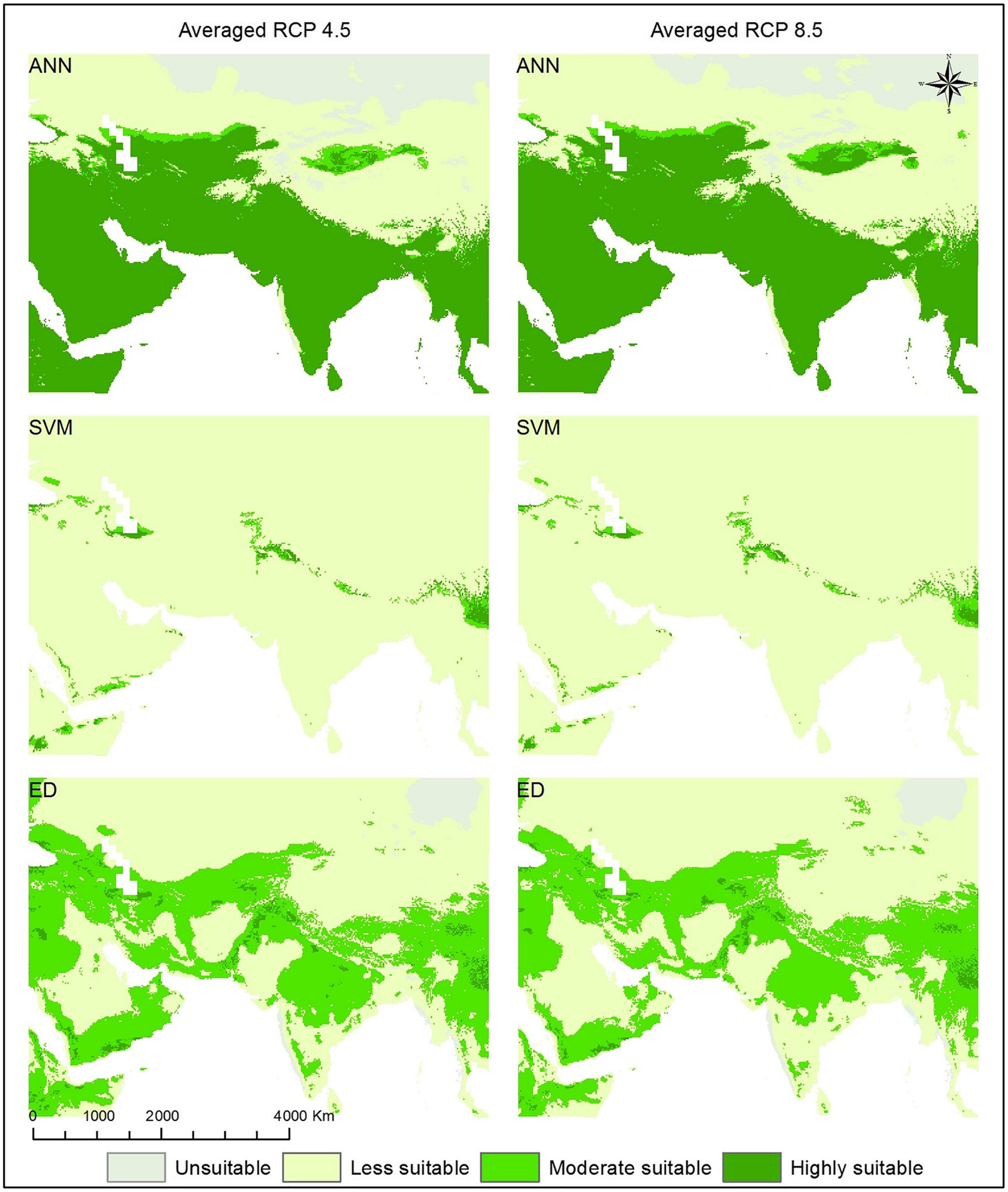

Fig. 5. Maps of modeled future potential distribution for *Olea europaea* sensu lato from artificial neural networks, support-vector machines, and environmental distance approaches (left side: RCP 4.5; right side: RCP 8.5).

Table 3. Cumulative comparison of total suitable area (%) for current and future projected RCP scenarios for *Olea europaea* sensu lato.

Models	Classes	Current (%) Global (10′)	Current (%) Central Asia (2.5′)	Future (%) Averaged (RCP 4.5)	Future (%) Averaged (RCP 8.5)
Maxent	Unsuitable	0.00	0.01	0.00	0.00
	Less suitable	88.04	88.03	96.58	97.00
	Moderately suitable	6.06	6.06	2.24	1.94
	Highly suitable	5.90	5.90	1.18	1.06
GARP	Unsuitable	75.88	73.36	67.66	66.82
	Less suitable	4.56	9.18	17.90	19.49
	Moderately suitable	8.92	12.44	9.63	8.98
	Highly suitable	10.64	5.03	4.82	4.71
BIOCLIM	Unsuitable	56.31	65.20	71.93	68.72
	Moderately suitable	43.68	34.79	6.14	31.28
	Highly suitable	0.01	0.00	21.93	0.00
ANN	Unsuitable	39.78	25.03	13.66	11.01
	Less suitable	14.32	26.69	34.74	35.95
	Moderately suitable	1.97	2.50	3.29	3.12
	Highly suitable	43.92	45.77	48.31	49.91
SVM	Unsuitable	0.00	0.00	0.00	0.00
	Less suitable	90.99	96.29	97.13	97.30
	Moderately suitable	4.39	2.38	1.92	1.92
	Highly suitable	4.62	1.33	0.95	0.77
Climate space	Unsuitable	0.19	0.54	0.46	0.48
	Less suitable	72.05	60.26	63.36	65.31
	Moderately suitable	13.22	25.91	25.37	24.15
	Highly suitable	14.55	13.30	10.82	10.07
Environment distance	Unsuitable	25.75	14.61	3.14	2.85
	Less suitable	31.32	38.38	58.21	61.33
	Moderately suitable	33.06	41.35	36.71	34.27
	Highly suitable	9.87	5.66	1.93	1.55

Note: GARP, genetic algorithm for rule-set prediction; ANN, artificial neural networks; SVM, support-vector machines.

under RCP 4.5 and 8.5, respectively (Table 3, Fig. 4). Genetic algorithm for rule-set prediction thus predicts the same general pattern as Maxent, but covering a larger area. BIOCLIM anticipated a much-broader area (~34.8% of the Asian study area), although thresholding is complicated by the fact that BIOCLIM predictions are very simple. BIOCLIM predictions with RCP 4.5 showed that highly suitable area increased, whereas with RCP 8.5 moderately suitable area decreased (Table 3, Fig. 4). ANN results were similarly broad, covering 45.8% of the Asian study area at present and increasing under future conditions by 2.5–4.1%. SVM results were closely similar in extent although somewhat different in position as those of Maxent: 1.33% of the Asian study area at present was identified as suitable declining to 1.0% with RCP 4.5 and 0.8% with RCP 8.5 (Table 3, Fig. 5). Environmental distance identified 5.7% of the Asian study area as suitable at present, declining to 1.9 and 1.6% under the two RCPs, respectively (Table 3, Fig. 4).

Conclusions and Recommendations

In this study, we have explored diverse approaches to estimating ecological niches for *O. europaea* sensu lato under present-day conditions and two scenarios of future climate. Although six of seven approaches yielded model predictions that were better than random (significantly so), Maxent and SVM emerged as the two approaches that showed good ability also to discriminate between suitable and unsuitable sites within our Asian study area, particularly given the limited range of the species in the region (Ashraf et al. 2016). These two approaches at least captured the limited distributional potential in the region, and thus were best able to discriminate between suitable and unsuitable areas, and avoid broad commission error.

As in previous such comparative analyses, the dominant theme that emerged was that results of climate projections for distributional shifts of species are highly method dependent (Pearson et al. 2006). The broad variation among approaches can be appreciated in our Figs. 4 and 5, in which very different future predictions emerged from different modeling approaches. Most indicated that likely future conditions will lead to at least moderate impacts on the species' distributional potential on our Asian study area. This species has been documented to be in the process of losing distributional area in some areas but gaining in other, higher-elevation areas (Ashraf et al. 2016).

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Supporting Information

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