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A revised map of plant geographical regions of the Southern Levant

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Abstract

We propose a revised map of plant geographical regions for the Southern Levant (most of Israel, the Palestinian Territories and Jordan). Since this region has been heavily impacted by human activity over millennia we have created a detailed natural vegetation map using GIS, remote sensing and a species distribution model (MAXENT). We created an extensive database of over 1800 historical and field observations for the region, incorporating plant species presence-only data, as well as environmental variables, including temperature and precipitation. Vegetation was modeled according to plant geographical regions and vegetation types. Our revised map generally agrees with previous vegetation maps done for the region, but provides more detail regarding the distribution of various forested communities that have been significantly disturbed by millennia of human activity. Given its digital format, this new map can be used for conservation and other applications that require a vegetation surface. It can also be used as a basis with which to model vegetated environments in past and future scenarios.

Keywords

Southern Levant, plant geographical regions, vegetation, species distribution model, Maxent

Author Bibliography

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1. Introduction

This study presents a revised map of plant geographical regions for the Southern Levant, a region where much of the vegetation has been altered over thousands of years. Our approach to mapping the natural vegetation using a maximum entropy model (MAXENT) is important for five reasons: (1) it utilizes presence-only vegetation observations to reconstruct the natural vegetation landscape of the region where little remains of the natural vegetation; (2) it provides a standardized vegetation map of the region where previous maps had focused on either the vegetation of Jordan or the vegetation of Israel and the Palestinian Territories; (3) it produces a digital vegetation map that can be used in applications that require digital vegetation surfaces (e.g., management applications); (5) it provides a basis for modelling more detailed vegetation maps (e.g., different forest types, different vegetation associations found throughout the desert region) and (5) it provides the foundation for comparing modern vegetation communities to future and past vegetation maps.

The authors are specifically interested in using this modern map as a training dataset to create paleo vegetation models and recreate the vegetation of this region throughout the Holocene (the geologic epoch that includes the last 12,000 years ago and in the Levant, a period that experienced dramatic climatic fluctuations as well as the rise and collapse of some of the earliest agrarian and urbanized societies) as well as project into future climatic scenarios. The trajectory of past vegetation in this region is important given the millennial history of complex human habitation in a setting that at present bears almost no resemblance to a supposedly heavily forested area during the early Holocene. Given the overwhelming reduction of forest areas (due to both climate change and human pressure), it is also important to model the vegetation under different climatic scenarios projected in the future, which can help to manage forest resources that are currently under pressure from grazing and other human activities (Al-Eisawi 2012) . MAXENT was chosen because it is the algorithm that best suits this objective of creating a present day model that can be trained to project into other geographic/temporal regions.

The study area lies at the junction of three continents (Asia, Europe and Africa) and four major plant geographical regions. As a result of its geographic position, the vegetation is extremely rich (Zohary and Feinbrun-Dothan 1966, Zohary 1973, Horowitz 1979, Al-Eisawi 1996, Danin 2004). This relatively small region includes a broad range of plant species from woodlands typical of moist Mediterranean climates, steppe vegetation typical of Eurasia, tropical desert oasis vegetation, and extreme desert vegetation that penetrates from North Africa and Saudi Arabia. The earliest vegetation maps of the main plant geographical regions were created by Eig (1931/32, 1938), and updated by Zohary (1962, 1966). Later maps were produced for Jordan by Al-Eisawi (1985), and for the lands west of the Rift Valley by Danin (1970, 1983) and Danin and Plitmann (1987).

2. Study Area

The study area encompasses about 42,650 km^2 between latitude 29°30’ N to 33°N and longitude 34°17’ E to 36°15’E (Figure 1). The region incorporates high topographic and climatic diversity. It extends from the Mediterranean Sea in the west across coastal plains and then ascends to the Central Hills (up to 1200 m). The study area then descends into the Rift Valley which extends from the Sea of Galilee in the north to the lowest place on Earth, the Dead Sea (- 410 m), to the Wadi Araba and then the Red Sea in the south. East of the Rift Valley lies the highest elevation landscape on the Jordanian Plateau (up to 1650 m), which is deeply incised by wadi valleys flowing west towards the rift. Beyond the plateau the landscape gives way to the Eastern Desert.

The region’s climate is Mediterranean, with long, dry and hot summers and wet, cool winters. Rainfall is most prevalent in winter and spring (November to May), although short and intense rain can occur during summer months, mainly affecting the more arid southern portion of the study region that receives less than 100mm/yr. The amount of precipitation in the study area decreases from west to east and from north to south, away from the Mediterranean Sea and south of the cyclonic storms that bring precipitation from the west. A second precipitation gradient is caused by topography, which contributes to the lowest amounts of precipitation being found in the Rift Valley and in the Eastern Desert. Temperature variation across the study area relates mainly to elevation and latitude. The coolest temperatures are found along the southern highlands on the Jordanian Plateau. Snow accumulation and freezing temperatures also can occur in the higher elevations. The warmest temperatures are found in the Wadi Araba, where they can reach 50°C (Al-Eisawi 1996).

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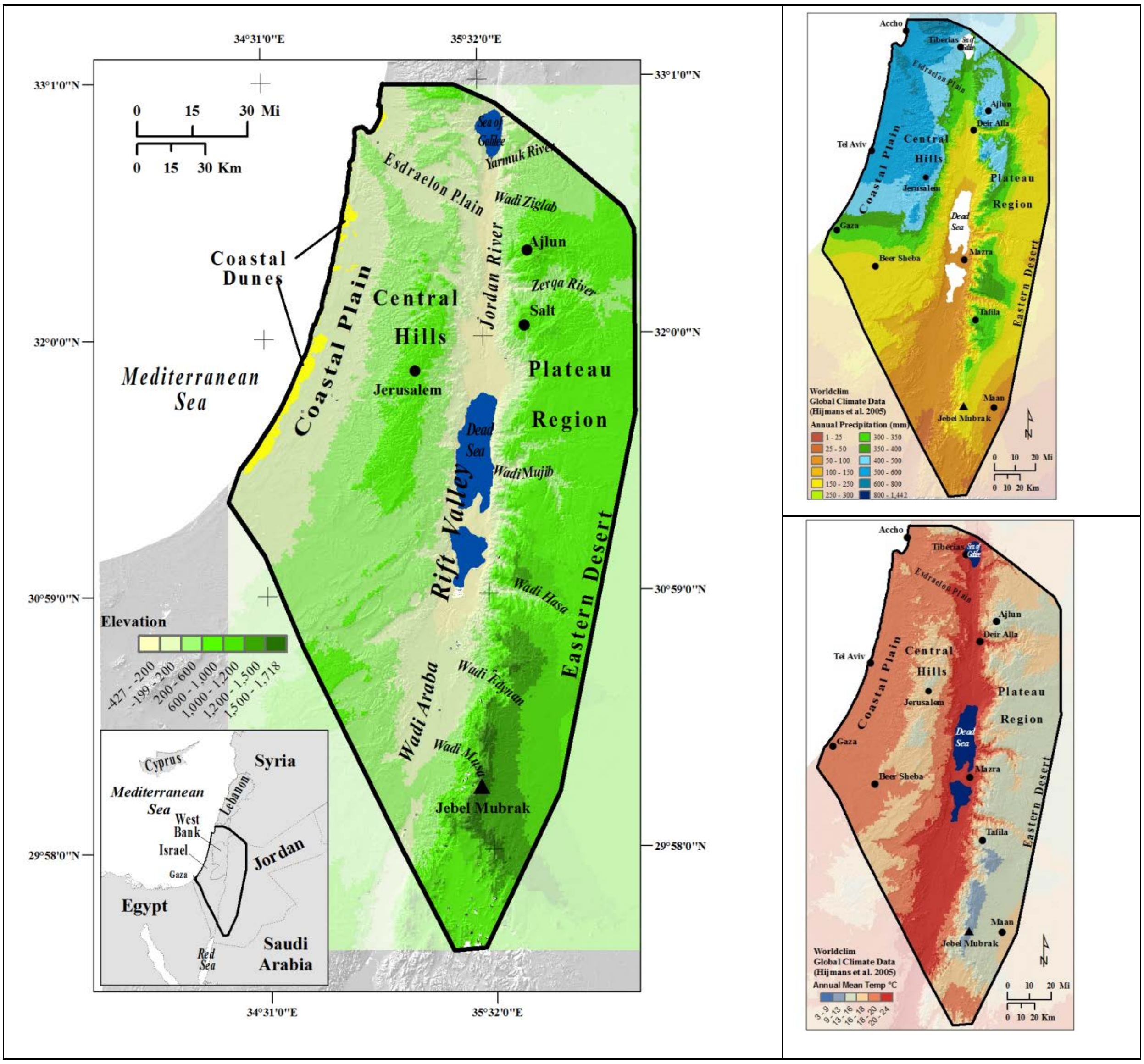

Figure 1. Major topographic features and elevation of the Southern Levant shown on left. Maps of mean annual precipitation and mean annual temperature shown on the right.

The study area includes four of the major vegetation zones found in the Middle East. These are the Mediterranean, Irano-Turanian, Saharo-Arabian and Sudano-Decanian, following Eig (1931/32, 1938) and Zohary (1962, 1968). Mediterranean vegetation grows in areas that experience the highest amounts of rainfall. Forests of pine (*Pinus halepensis*) and deciduous and evergreen oak (*Quercus ithaburensis* and *Q. calliprinos*) grow in the wettest areas near the Mediterranean and at higher elevations, particularly surrounding the Sea of Galilee and in the northwestern coastal region. More open woodlands are found in areas that receive less moisture both west of the Rift Valley where carob and pistacia (*Ceratonia siliqua* and *Pistacia lentiscus*) are found surrounding and penetrating the Central Hills, and east of the rift on the Southern Highlands of the Jordanian Plateau, which supports open woodlands of juniper (*Juniperus phoenica*) and evergreen oak (*Quercus calliprinos)*.

The Irano-Turanian region is distinguished by steppe vegetation that consists of grasses and shrubs. *Artemisia herba-alba* is the most common shrub species; other taxa include *Noaea mucronata, Retama raetam, Salsola vermiculata,* and *Anabasis syriaca*. Scattered *Pistacia atlantica* and *Juniperus phoenicia* trees can also be found with an understory typical of steppe vegetation. This region, which sits along a transition zone between the more humid Mediterranean and the more arid Saharo-Arabian regions, receives 150 to 350 mm/yr of rainfall. Temperatures in the Irano-Turanian region are more extreme, with hotter summers and colder winters than are found in the Mediterranean region. Mean annual maximum and minimum temperatures range from 12-25°C and 5-20°C (Al-Eisawi et al. 2000).

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The Saharo-Arabian region, where precipitation rarely exceeds 200 mm/yr, is characterized by drought tolerate plant species. It is found along the Rift Valley, in the Negev Desert and in the Eastern Desert on the plateau. This region experiences the most extreme annual temperature fluctuations with mean annual minimum and maximum temperatures in the Rift Valley ranging between 10-20 and 20-35°C, respectively (Al-Eisawi et al. 2000). Summers are extremely dry, although seasonal storms from Africa may bring sudden storms with high amounts of runoff. The driest area occurs in the Wadi Araba in the southern part of the Rift Valley, where annual precipitation is less than 50 mm/yr, and in the Eastern Desert, which receives around 100 mm/yr. The vegetation typically found in this region is manifested in diffused (e.g., spread out on slopes or depressions) or contracted (for example along wadis) patterns, and is ultimately dependent on water availability. Common plants found throughout this region include *Zygophyllum dumosum, Haloxylon articulatum, Anabasis articulata, Anabasis syriaca, Astragalus spinosus, Suaeda palaestina*, *Salsola tetrandra*, *S. asphaltica*, and *Achillea fragrantissima*. Riparian species like *Tamarix sp., Phragmites sp.*, *Salix sp.*, and *Nerium oleander* are also found along wadis. For instance, a riparian forest of *Populus euphratica Tamaricetum jordanis* grows along the banks of the Jordan River (Eig 1938).

Sudano-Decanian vegetation is restricted to pockets along the Rift Valley from the Gulf of Aqaba north along the Jordan Valley to Deir ‘Alla, which are the hottest locations in the region. The most common species include *Acacia spp., Ziziphus spina-christi, Balanites aegyptica, Moringa aptera, Ocradenus baccatus, Salvadora persica* and *Calotropis procera*, and represent the northern extent of tropical African vegetation.

3. Methods

In this study, plant geographical regions were mapped using species distribution modelling or SDM. This allows the distributions of species to be mapped across geographic space using a set of occurrences and environmental or predictor variables that characterize them (Franklin 1995). As a result of innovative and more accessible statistical and GIS tools, as well as more available data from museums, herbarium collections and online databases (for example, GBIF http://data.gbif.org/), SDM has been growing in popularity during recent years in fields like conservation science, planning, evolution biogeography, and ecology (e.g. Elith et al. 2003; Freeley & Silman 2010; Guisan & Zimmermann 2000; Kremen et al. 2007; Illoldi-Rangel et al. 2012). The steps in building a species distribution model include obtaining observations and predictor variables, determining if any variables are correlated, choosing an algorithm with which to model the distribution, calibrating the algorithm, choosing a threshold if the output needs to be converted to a presence/absence map, and determining how the model will be evaluated. This section describes the steps followed in order to build a SDM models of plant geographical regions in the Southern Levant and how these were combined into a map of present day plant geographical regions.

To model plant geographical regions, indicator species for each region were sourced from the literature (Al-Eisawi 1998; Eig 1931/32, 1938, 1946; Danin 1988, 1999; Kasapligil 1956; Zohary 1973). A database of 1804 plant species observations located throughout the study area (Figure 2) was then created by conducting field work, digitizing data from vegetation transects surveyed at different times during the last 125 years (Davies & Fall 2001; Eig 1946; Kasapligil 1956; Qishawi et al. 1999; Post 1886; Zohary 1944, 1973) and compiling observations from herbarium collections (BioGIS 2000 and BioGIS 2002). Some of the earliest observations were collected prior to the establishment of present day international borders and also precede the widespread intensification and industrialization of irrigation agriculture and the energy intensive green revolution technology that characterizes large areas of the modern landscape of the region. These data are invaluable for recreating the natural vegetation for regions like the modern Middle East whose landscapes have been transformed dramatically over the past few decades.

To optimize regional sampling and to minimize data gaps evident after entering the historical observations and recent surveys (Davies & Fall 2001 and Qishawi et al. 1999), we conducted strategic queries utilizing the Israel Biodiversity Information System database. This resource synthesizes thousands of records for plants and animals in Israel and the West Bank obtained from museum and herbarium collections, as well as from surveys done by academic institutions, governments, and non government organizations that contributed data from 470 additional samples (BioGIS 2000 and BioGIS 2002). To pursue the same goals for regions east of the Rift Valley, we conducted field work during the Spring of 2010. A series of latitudinal transects produced data from 194 further locations, which were sampled from low to high elevations throughout the study area east of the Rift Valley (Figure 2). This fieldwork also allowed us to validate data from 20 historical observations that we had digitized from Eig and Zohary.

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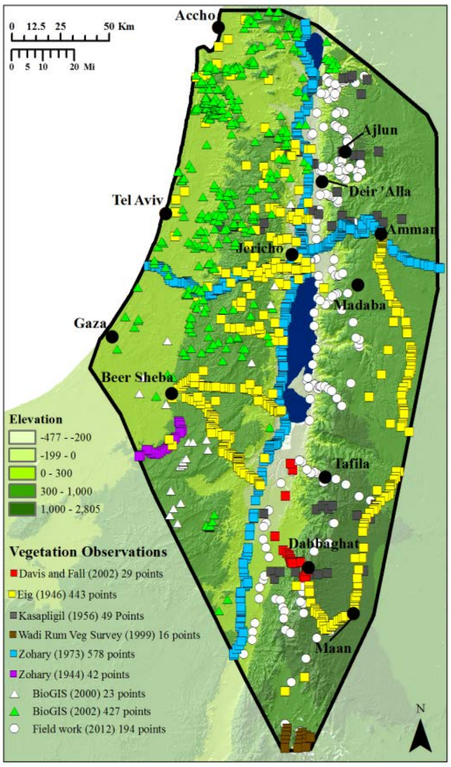

Figure 2. Observations database built for this study.

Except for the Tropical Sudanian Zone, which includes plants that are mainly influenced by edaphic factors, most indicator plants are related to their vegetation zone based on climatic and topographic factors. On this basis we selected the following environmental variables at a 1 km spatial resolution: geology, elevation, a series of climatic variables described below, rivers, and springs. For similar applications of these variables see Austin et al. 1994; Brzeziecki et al. 1993; Franklin et al. 1986; Palmer & Van Staden 1992.

Elevation, slope and aspect were obtained from high resolution digital elevation models (DEM) derived from 2002 Terra ASTER satellite imagery (http://asterweb.jpl.nasa.gov), which includes a 15m resolution band (Band 3) taken with forward and backward cameras that can be processed into DEM. The DEM were resampled from a 90-m spatial resolution to 1km. Regional geology was digitized from a 1:200,000 geological map of Israel (Sneh et al. 1998) and a 1:750,000 geological photomap of Israel and adjacent areas (Bartov 1994). The climatic variables were derived from a Macrophysical Climate Model or MCM (Bryson & DeWall 2007) that is being used to investigate long term social, environmental and ecological interactions in the Mediterranean Basin during the Holocene by reconstructing and modeling past environments (e.g., Barton et al. 2004, Barton et al. 2010). The variables were assessed for spatial autocorrelation using the MAKESTACK command in ArcGIS 9.3. Variables that were highly correlated (>0.85) were removed (for instance, average summer temperature and average winter temperature proved to be highly correlated with the temperature of the warmest and coldest month, and were therefore not utilized; the latter two were used because they represent extremes and can better capture the species that fall in this range).

Supplemental literature indicates that the vegetation found within the Tropical Sudanian region is mainly restricted to areas in the Rift Valley that experience extremely hot temperatures and water (given the presence of rivers and springs). A shapefile of spring locations was created by querying 'springs' from the Geographic Names Server (GEOnet Names Server) for Israel, Jordan and the West Bank. These were then buffered and a grid file was created showing the area surrounding these springs at several distances (2, 4, 6, 8, greater than 8km). The rivers were also buffered at 1, 2, 3, and 5 km (see below for a description of how this layer was created). Since this vegetation is only found in the Araba Valley and Lower Jordan Valley, a mask was used outside these areas.

MAXENT was chosen over other modeling tools because it performs as well as or better than other methods for modeling species distributions (e.g., Elith et al 2006; Hernandez et al. 2006, Hijmans and Graham 2006). Among its advantages, MAXENT accommodates 'presence-only' data like those available for this study (replaces absence with background information); the default parameters used to calibrate the model have been tested with large datasets (Phillips and Dudík 2008); it uses both continuous and categorical variables; it can perform well when using low numbers of occurrence records (Hernandez et al. 2006); is capable of extrapolating into past and future scenarios and has internal mechanisms that estimate uncertainty produced by conditions that are different from those used for training the model (e.g., Elith et al. 2011; Hernandez et al. 2006; Hijmans and Graham 2006;

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VanDerWal et al. 2009); it has a series of internal validation methods; and it can be implemented through a software tool that is free and available via the world wide web (http://www.cs.princeton.edu/~schapire/MaxEnt).

Maxent version 3.3.3e was calibrated using the settings recommended by Phillips et al. (2006), the observations, variables, and settings shown in Table 2. The models were trained with the observations and 10,000 randomly selected background points from a 1km grid across the study area, unless otherwise specified (bias grids were used for some models). Because there were large numbers of observations available for the Mediterranean, Saharo Arabian, and Irano Turanian models (Table 2), the datasets were divided into training and testing subsets using a split sample approach (Fielding and Bell 1997). The Tropical Sudanian category, on the other hand, had few observations so they were split into samples using 10-fold cross validation, which is an effective way to evaluate the models' predictive output (Elith and Leathwick 2009) and ensures all observations are used to train the model (Elith and Leathwick 2009).

Zone	**Testing Method**	**# Training samples**	**# Test samples**	**Bias file used**	**Settings and notes**
Mediterranean	Data partition. Random 60% used for training, 40% used for testing.	351	234	No	**Environmental layers used**: annprec anntemp elev geol3(categorical) mask **Regularization values**: linear/quadratic/product: 0.050, categorical: 0.250, threshold: 1.000, hinge: 0.500 **Feature types used**: P L Q H T
Saharo Arabian	Data partition. Random 75% used for training, 25% used for testing.	294	98	Yes	**Environmental layers used**: annprec anntemp elev geol3(categorical) mask **Regularization values**: linear/quadratic/product: 0.050, categorical: 0.250, threshold: 1.000, hinge: 0.500 **Feature types used**: P L Q H T
Irano Turanian	Data partition. Random 75% used for training, 25% used for testing.	225	74	Yes	Environmental layers used: annprec anntemp elev geol3(categorical) mask Regularization values: linear/quadratic/product: 0.050, categorical: 0.250, threshold: 1.000, hinge: 0.500 Feature types used: P L Q H T
Tropical Sudanian	Resampling, 10-fold crossvalidation	43	5	490	**Environmental layers used:** alt annprec anntemp julytemp mask rivers1(categorical) springs(categorical) **Regularization values**: linear/quadratic/product: 0.213, categorical: 0.250, threshold: 1.570, hinge: 0.500 **Feature types used**: L Q H

Table 2. Maxent calibration settings.

The Maxent outputs are given as a continuous surface, in which each cell has a value that is part of the distribution found by the model and indicates likelihood of presence. To create a binary map showing where the presence is most likely to occur, a threshold or cut-off value must be chosen. Depending on what value is chosen, the output can be extremely different, and impact the area over which a species is predicted (this may be expressed as prevalence, which can be calculated by dividing the cells in which the species is present by the total number of cells). This has obvious implications for both errors of omission and errors of commission. The smaller the threshold, the smaller the omission error will be (but at the expense of greater commission error). As the threshold becomes bigger, errors of omission increase whilst those of commission decrease (Fielding and Bell 1997).

The threshold that maximizes the sum of sensitivity and specificity was chosen to convert the continuous output produced by MaxEnt into a binary surface that distinguishes suitable versus unsuitable areas. This threshold is based on the point in the Receiver Operating Curve (ROC) where the sum of sensitivity and specificity is maximized (Manel et al. 2001) and the mean of the error rate of presences and absences is minimized (Freeman and Moisen 2008). The ROC is produced by plotting sensitivity on the *y* axis against *1* minus specificity across different thresholds on the *x* axis (1-specificity is also known as the false positive rate and represents errors of commission, whereas specificity, also known as the true negative fraction, refers to the proportion of observed absence or pseudo absence records correctly predicted as absence). Sensitivity refers to the observations that are correctly classified and indicates the sensitivity of the model for predicting observations where they actually occur, while specificity refers to how well the model can predict true absences. Determination of a threshold in this manner makes use of the ROC curve, minimizes the mean of the error rate of presences and absences (or pseudo absences in the case of MaxEnt) (Manel et al. 2001, Freeman & Moisen 2008), and has proven superior to other methods for establishing modelling thresholds (Liu et al. 2005).

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After the vegetation zones were modeled, they were combined to produce one plant geographical region map for the southern Levant. For the most part the distributions of the different zones don't overlap. However, when a particular cell does overlap it is assigned to a transition zone or ecotone (Mediterranean-Irano Turanian or Irano Turanian-Saharo Arabian transition zone).

Because there is no consensus in the literature regarding the best way to evaluate SDM models based on presence-only data (Hirzel et al. 2006), the models were validated using a variety of measures and statistics to evaluate different aspects of the models' performance. In particular, the performance of the model was assessed through the *omission rate* and the *proportional predicted area* (Phillips et al. 2006) for the purpose of determining whether the output is better than could have been predicted by chance (Anderson et al. 2002). A one-tailed binomial or a chi-square test assessed the statistical significance of obtaining the resulting omission rate by chance or sampling error (Anderson et al. 2002). This method tests the null hypothesis that, given the fractional area predicted, the test points are predicted no better than if they had been predicted by chance (Elith 2008).

Model performance across all thresholds also was examined using the area under the curve (AUC), which is a measure used commonly in species distribution modeling to evaluate a model's predictive ability (Hanley and McNeil 1982, Fielding and Bell 1997), by indicating how well the model is able to discriminate where a species is present versus where it is absent. Because Maxent has no information regarding absences (as mentioned previously), it uses randomly selected 'pseudo-absences' instead (Phillips et al. 2006). This performance is rated between 0 and 1 when presence/absence information is used. However when pseudo absences are used, the highest value is $1 – a/2$, in which a is the portion of cells occupied by the species. Because a is unkown, it is not possible to determine the optimal value. This statistic indicates how well the model is able to distinguish a true presence from a randomly chosen point. A value of one means the model was able to discriminate completely, a value of 0.5 means the model's discriminative performance was the same as a random guess, a value smaller than 0.5 means the model's discriminative performance was worse than a random guess (Elith et al. 2006). Species with narrow distributions (with regard to the study area) are expected to have higher AUC values. As a rule of thumb (Swets 1998), an AUC between 0.5 – 0.7 indicates low accuracy, 0.7 – 0.8 suggests the model accuracy is fair, 0.8-0.9 is good, and values greater than 0.9 represent excellent model accuracy. Overall, AUC values above 0.75 are considered potentially useful (Elith 2002). Maxent also has a series of internal validation methods that facilitate the interpretation of variable performance amongst models. A jackknife test estimates the importance of the different variables and calculates response curves that show how the prediction relates to particular variables, as well as which variables are most important when training the model.

4. Results

The resulting map of present day plant geographical regions is shown in Figure 3. The combination of the plant geographical regions into one map created two additional transition zones between the Mediterranean and Irano Turanian regions (M-IT), and between the Irano Turanian and Saharo Arabian (IT-SA) regions.

The region of Mediterranean vegetation occupies the wetter, higher elevation portions of the study area on both sides of the Rift Valley. On the west, the Mediterranean region is more continuous and spreads south until it reaches the northern Negev. East of the Rift Valley, the Mediterranean region is not as extensive as its coastal counterpart, although it is still the dominant region in the northern portion of the Jordanian Plateau. Farther south, a few patches of Mediterranean vegetation are found in the Southern Highlands of the Plateau.

The M-IT zone lies alongside the larger Mediterranean region with a few additional patches in the Negev Highlands, at the edge of the study area. The Irano Turanian region (which represents steppe vegetation and is characterized by small shrubs and bushes and a lack of trees) sits between the Mediterranean and Saharo Arabian regions. On the Jordanian Plateau it interrupts the longitudinal Mediterranean belt in some of the valleys (e.g., Wadi Mujib) that drain west into the lower elevations of the Rift Valley. This region is also prominent on the higher elevation areas of the Negev.

The Saharo Arabian zone spreads throughout the Wadi Araba, north into the Negev and the Jordan Valley, as well as along the easternmost fringe of the study area, marking the beginning of the Eastern Desert of Jordan. The IT-SA zone is found in the Rift Valley between the Saharo Arabian and Irano Turanian zones, as well as on the southern Jordanian Plateau region in Wadi Mujib and Wadi Hasa, and in patches in the Negev Highlands and southern Negev. Tropical Sudanian vegetation is found in pockets around the Dead Sea and along the Jordan Valley.

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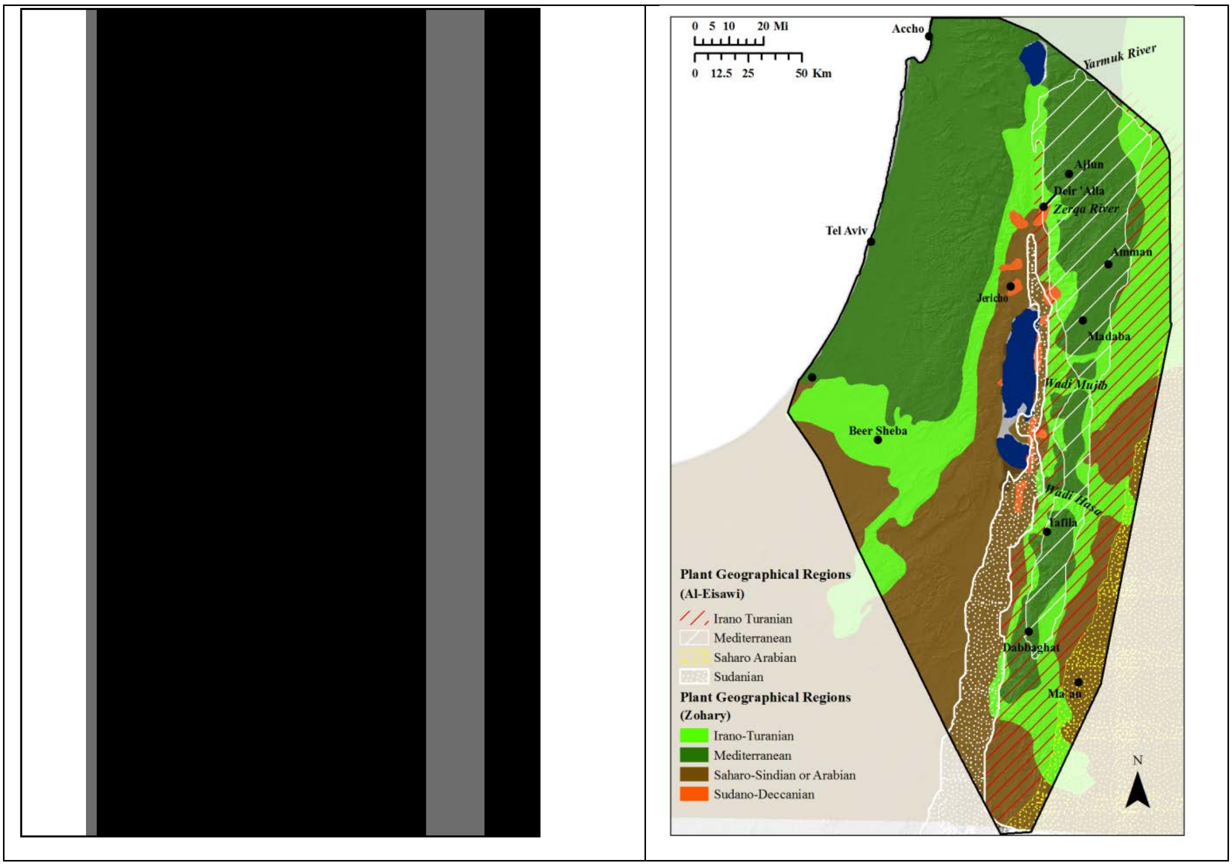

Figure 3. Modern map of plant geographical regions of the Southern Levant according to modeling done in this study (left) and maps created by other authors (right).

4.1. Model evaluation

Table 3 presents an evaluation of model performance across the selected threshold, as well as across all thresholds (based on AUC). AUC values over 0.75 indicate that the models for all four vegetation types show acceptable performance (Pearce and Ferrier 2000). P-values indicate the probability of obtaining an observed omission rate due to random chance or sampling error (Anderson et al. 2002), given the threshold that was used to create binary surfaces (the one that maximizes the sum of sensitivity and specificity). These evaluation results include the logistic values at which the threshold was met in modeling each vegetation type, the fractional areas predicted according to the threshold, omission error rates for the observations used for training, omission error rates for the observations set aside for testing, and the statistical significance of each prediction. The models for all four vegetation types performed better than if they had been generated by chance, as indicated by P-values less than 0.05. Mediterranean vegetation is predicted for the largest portion of the study area (as indicated by its fractional predicted area). This result may seem unexpected in light of the disturbed condition of modern forests and their association with early successional vegetation (batha and garigue). Nevertheless, our modelling predicts that, if left undisturbed, Mediterranean vegetation would potentially occupy the largest portion of the study area.

	Omission rate and the proportional predicted area according to threshold					**Performance according to AUC**		
Category	**Logistic threshold***	**Fractional predicted area**	**Training omission rate**	**Test omission rate**	**P- value**	**Test AUC**	**SD**	**Performance (Swets 1998)**
Irano Turanian	0.397	0.251	0.173	0.216	1.90 E-26	0.789	0.02	**Fair**
Saharo Arabian	0.272	0.341	0.044	0.082	8.83 E-34	0.803	0.014	**Good**
Mediterranean	0.253	0.374	0.06	0.085	0.00 E+ 00	0.831	0.009	**Good**
Tropical Sudanian*	0.2478	0.1028	0.13	0	1.20 E-04	0.9522	0.016	**Excellent**

* 10 fold cross validation

Table 3. Threshold evaluation and model performance based on AUC.

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4.2. Variable importance

The relative importance of the variables used in this modeling may be assessed using assessments produced by MaxEnt (e.g., percent variable contribution table, jackknife plots of variable importance, variable response curves). The most important variable in determining suitable areas for all plant geographical regions is mean annual rainfall. This variable is ranked at the top in percent contribution and permutation importance. The jackknife test of variable importance also shows that this variable allows a good fit to the training data when used alone. When omitted, it decreases the gain for the Mediterranean and Saharo Arabian categories. The response curve plots show how this variable relates to each category. For the Mediterranean category, the gain starts to increase steadily above 300 mm/yr. For the Irano Turanian region, it peaks between 200 and 400 mm/yr. For the Saharo Arabian region, on the other hand, suitability decreases dramatically as rainfall increases. This suggests that this variable will be crucial when creating models of vegetation in past and future scenarios.

The second most important variable, however, was different for each category. For the Mediterranean region this variable was geologic substrate (limestone), which was followed closely by annual temperature. For the Irano Turanian and Saharo Arabian categories, the second most important variable is annual temperature, followed by elevation (Irano Turanian) and geology (Saharo Arabian). Elevation also was important for Tropical Sudanian vegetation, in accordance with its distribution in the lower elevation areas of the Rift Valley. However, when omitting this variable, the gain of the model was reduced only modestly, suggesting that the information contributed by this variable is captured by other variables. Average annual temperature and distance to rivers and springs also were important variables when modelling this category.

5. Discussion

Although the region suitable for Mediterranean vegetation shows general agreement with Eig's (1931/32) and Zohary's (1962, 1966) delineation of this territory, our modelling shows several noteworthy differences. For instance, Zohary includes the entire coastal plain within the Mediterranean vegetation region, whereas our results propose Mediterranean vegetation only for the northern portion of the coastal plain. This area has been heavily impacted by urban development. Nevertheless, the communities that are found throughout this area (now quite fragmented and as remnant stands) include both evergreen and deciduous oak maquis as well as pistacia and carob woodlands. The modeled distribution of Mediterranean vegetation for the remaining coastal plain is fragmented, particularly in the far south. Throughout this area, the vegetation acquires more of a Mediterranean savannoid character, with *Ziziphus spina Christi* and *Ziziphus lotus* trees becoming more abundant. In his map of natural environments, Horowitz shows a thin strip (about 5 km wide) adjacent to the coastal sand dunes as Saharo Arabian (Horowitz 1979: 28). On the eastern slopes of the Central Hills Zohary draws the boundary of the Mediterranean region at the edge of the Judean Desert, whereas our modelling extends Mediterranean vegetation slightly into the Judean Desert (which Zohary classified as Irano Turanian). On the Plateau, the Mediterranean region covers a smaller area than that depicted by Zohary. Modern vegetation here includes juniper, oak, cypress, and pistachio trees. Al-Eisawi's map shows Mediterranean vegetation on the Jordanian Plateau as an uninterrupted strip of varying width stretching from north to south. Zohary's map and ours extend the Mediterranean zone about 20 km farther south.

The Irano Turanian vegetation region produced by our modelling resembles the area delineated by Eig (1931/32) and Zohary (1962, 1966) to a large extent, with some variations. MaxEnt modelling predicts this region along the northern portion of the Rift Valley, from the Sea of Galilee to the Lower Jordan Valley. As with the Saharo Arabian region, most of the disagreement between vegetation studies arises on the Jordanian Plateau. Our modelling predicts a larger area of Irano Turanian vegetation on the northern Plateau than proposed by Zohary (1962) and Al-Eisawi (1966), but a smaller area than plotted by Zohary and Al-Eisawi on the southern Plateau.

Our modeled Saharo Arabian plant geographical region is quite similar to the area delineated in other maps. For instance, Zohary (1962) shows almost the same extent in the Rift Valley and adjacent areas. Our model extends this region slightly farther north (Zohary's stops at Deir 'Alla whereas Al-Eisawi's ends a few kilometres south of Deir 'Alla) and expands it into adjacent wadis (which is missed by other maps). Except for the Northern Negev, which Zohary classified as Irano Turanian, the remaining Negev subdivisions are almost identical with Zohary's map. Southeast of the Rift Valley, Zohary shows the Saharo Arabian region expanding onto the Jordanian Plateau (just north of Wadi Rum) in agreement with our modelling. Al-Eisawi plots Saharo Arabian vegetation in the Rift Valley over an area slightly tighter than ours. The most divergent plotting of Saharo Arabian vegetation occurs on the Jordanian Plateau, where each map depicts varying widths and extents.

In keeping with our modelling, other authors identify Tropical Sudanian enclaves surrounding the Dead Sea and along the Lower Jordan Valley. Al-Eisawi notes this vegetation between Aqaba and Deir 'Alla, but adds that it is most prominent in the area surrounding the Dead Sea (hotspots include Ghor Safi and Ghor Faifa). Danin's map attributes only small areas to this category. Like Al-Eisawi, Zohary (1947) mentions oases with this vegetation along the Dead Sea and Lower Jordan Valley. In its northern distributions, Tropical Sudanian vegetation commonly includes *Ziziphus spina Christi, Balanites aegyptica*, *Callotropis procera*, *Acacia tortilis* and *Acacia albida*. In addition to these taxa, southern Tropical Sudanian distributions include *Phoenix dactylifera*, *Salvadora persica*, *Moringa aptera*, *Occradenus baccata* and *Nerium oleander*. Our application of Maxent utilized the

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northernmost observations of tropical oasis vegetation (Zohary 1973), and predicted a potential distribution of this vegetation about 20 km farther north. Indeed, Zohary (1947) mentions remnants of *Acacia albidae* in a few locales (e.g., Wadi Taiba) at the northern extent of the area predicted by Maxent, reinforcing the likelihood that this type of vegetation once spread over a greater area.

6. Conclusion

Maxent modelling predicts the potential modern distribution of four major vegetation types across the southern Levant with high rates of model performance. The contributions of key environmental and climatic variables differ considerably between the models for these vegetation types. While predicting vegetation distributions in keeping with previous vegetation mapping studies, our modeled potential vegetation patterns diverge in a variety of sometimes counterintuitive ways that hold implications for further modelling of present and past vegetation in this region.

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