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Long-term climate forcings to assess vulnerability in North Africa dry argan woodlands

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Abstract

Questions: North African dry woodlands constitute mediterranean climatic ecotone ecosystems of vital importance for human livelihoods and local biodiversity. To improve the basis for managing these key ecosystems, we selected a Tertiary relict woodland (*Argania spinosa*) in order to clarify the sensitivity to long-term climate change (the present, the past glacial-interglacial cycle and under future scenarios). We also discuss the impact of long-term human land use for the distribution of dry woodlands in North Africa.

Location: North Africa.

Methods: To assess whether the argan woodland is in equilibrium with current climate, we used species distribution modelling (SDM) to estimate its potential range. Then, SDM was used to estimate its potential distribution during the Last Glacial Maximum (LGM; 21,000 BP) and the Middle Holocene (Mid-Holocene; 6,000 BP). Model predictions for past scenarios were compared with Quaternary palaeorecords to evaluate their accuracy. Finally, we forecasted changes in the potential range to year 2080 to assess its likely future range dynamics.

Results: At the LGM, suitable areas occurred at more southern latitudes, where the Sahara Desert currently lies, while suitable areas in the Mid-Holocene shifted northwards, occupying areas similar to those of today. The estimated past distributions are consistent with palaeorecords, providing evidence for the important role of Quaternary climate changes in driving dry woodland range dynamics. The current range-filling constitutes 44% of the potential distribution, probably primarily reflecting anthropic land-use effects. Future climate change is forecast not to cause latitudinal/altitudinal range shifts, but rather an overall range contraction.

Conclusions: The models reflect the high sensitivity of the dry woodland ecosystem to past climate changes, in agreement with palaeorecords. The estimated climatic sensitivity also predicts severe range contraction during future climate change. Consequently, management strategies for dry woodlands should be developed to facilitate their *in situ* survival, particularly by reducing the currently intensive human pressure.

Introduction

A global overview reveals that warming and decreased water supplies are the main risk factors for tree losses and forest dieback (Allen et al. 2010). Drought-induced tree mortality has now reached rates that lead some authors to suggest that the world may already be entering “a new era of tree death and forest transformation” (Birdsey & Pan 2011). Drought impact may be particularly drastic in areas already subject to a high degree of aridity stress, where water is the most important limiting resource (Peñuelas & Boada 2003). Dryland forests account for 6% of the world’s forests and provide key ecosystems for human livelihoods to over one thousand million people living within the arid and semi-arid climatic zones (Safriel 2007). However, to date, the degradation of arid and semi-arid forests in areas of high human population density and its interaction with climate change have not received special

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attention from the scientific community (López-Sáez & Alba-Sánchez 2009; Le Polain de Waroux & Lambin 2012), despite its importance for biodiversity conservation as well as human livelihoods (Lybbert et al. 2011).

North African dryland forests, part of the mediterranean biogeographic region, are already facing the consequences of ongoing climate change (climate warming and water stress), as well as intense human pressure (Allen 2003). Studies on the relationship between environmental changes and human impact have indicated that in the Mediterranean Basin the level of human activities remains the most worrying problem for biodiversity (Blondel & Médail 2009). Indeed, the 25% of Mediterranean refugia areas, which are 'phylogeographic hotspots' and significant reservoirs of genetic diversity, are currently under severe threat from human influence (>250 inhabitants·km^{-2}), mainly along the coasts (Médail & Diadema 2009).

Among these endangered ecosystems are the argan [*Argania spinosa* (L.) Skeels] woodlands (Benabid 1985), which constitute a characteristic ecosystem for the Western Mediterranean region (southwest Morocco) at the edge of the Sahara Desert (Bani-Aameur et al. 1999). Argan woodlands are still relatively extensive (1 million ha), but rapidly declining as a result of anthropic disturbance (overgrazing, deforestation) and desertification as consequence of climatic stress (Prendergast & Walker 1992; Tarrier & Benzyane 2003).

Argan woodlands also provide a useful illustration of a climatic ecotone ecosystem of key importance for human livelihoods, as well as a key element of local biodiversity in North Africa. These woodlands have presumably been influenced by past climate change and are likely to be influenced by future climate change within the next century (Belyazid 2000). Additionally, in less than a century, more than a third of the argan woodlands have disappeared due to overexploitation for high-quality charcoal and conversion to agriculture (Le Polain de Waroux & Lambin 2012). The argan woodlands support more than 3 million Berbers, and nearly 90% of the economy in the region depends on argan agroforestry (Tarrier & Benzyane 2003). Indeed, Morocco's argan oil is now the most expensive edible oil in the world. However, Lybbert et al. (2011) suggest that booming argan prices have not improved the argan woodlands conservation and may even have induced or increased the process of degradation.

Furthermore, *A. spinosa* is the only representative of the amphi-Atlantic tropical/subtropical family Sapotaceae in northwest Africa (Pennington 1991) and could be considered a Mediterranean Tertiary relict tree, given both its evolutionary singularity (Petit et al. 1998) and its geographic rarity. It furthermore has high habitat specificity (Msanda et al. 2005), perhaps reflecting its evolutionary adaptation to semi-arid environments.

Given the forecasts that arid and semi-arid areas will be strongly affected by near-future drought stress (Peñuelas et al. 2004), a careful climate sensitivity assessment is needed for the argan woodlands in order to understand and counteract their future risk exposure. Here, we assess the possible shifts of argan woodlands in North Africa since the Last Glacial Maximum (LGM; 21,000 BP). Based on a review of the Quaternary fossil evidence for the distribution of *A. spinosa*, as well as preceding studies on the structure of argan population genetics (El Mousadik & Petit 1996a,b; Petit et al. 1998), we hypothesise that argan woodlands were not widely distributed in Morocco during the Late Quaternary, as opposed to the conclusions of previous studies (Benabid 1985). Rather, the range of this species would have extended, during the Last Glacial Maximum, to more southern latitudes than at present.

Using species distribution modelling (SDM) and a systematic review of Quaternary palaeorecords, we aim to: (i) assess the impact of late Quaternary climate change (LGM, ca. 21 ka, and mid-Holocene, ca. 6 ka) on the past potential distribution of argan woodlands; then (ii) using SDM, determine which current climatic factors limit the present-day distribution of argan woodlands; and finally (iii) predict the likely consequences of future climate change for this ecosystem.

Methods

Study area

Morocco (28–36° N, 2–12° W) lies in the Western Mediterranean region, on the northwest coast of Africa and is bordered by Mauritania to the south and Algeria to the east. Morocco's varied geography includes four separate mountain ranges, in addition to fertile river valleys, hundreds of kilometres of coastline and wide expanses of desert. The three most prominent mountain ranges (subranges of the Atlas Mountains) are the Middle Atlas, the High Atlas and the Anti-Atlas (Fig. 1). The Atlas Mountains separate the Mediterranean and Atlantic coastlines from the Sahara Desert, and constitute one of the distinct physiographic provinces of the larger African Alpine System division.

Current climate

Morocco's climate is mediterranean, but also falls under Atlantic and Saharan influences. Two gradients characterize this climate: decreasing precipitation with increasing temperature from north to south and from west to east (Le Houérou 1986). In the north, rainfall varies between 800 mm and 2000 mm, reaching maximum values on the northwest Atlantic coast; while on the edge of western Sahara, precipitation is as low as 100–400 mm. In addition,

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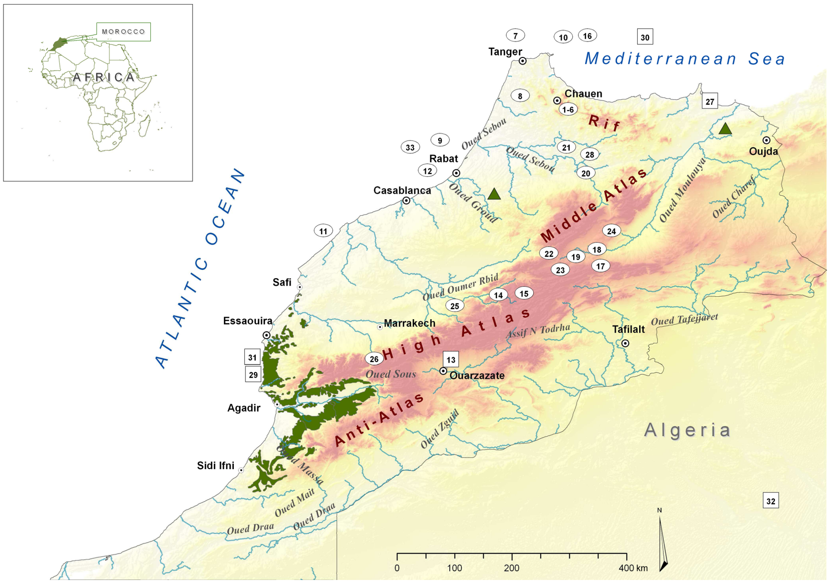

Fig. 1. Geographic distribution of Argania spinosa (main range: green shape; isolated population: green triangles) in Morocco. Location of Quaternary pollen records (squares indicate records with presence of argan pollen, oval figures, no presence): 1. Daya Arbatete; 2. Bab Taza/Fifi; 3. Marzine; 4. Tanakob; 5. Bou-Hachem; 6. Jbel Tizirene; 7. El-Khil; 8. Zerga; 9. Bokka; 10. Kaf That El-Ghar; 11. Oualidia; 12. Sidi Bou Rhaba; 13. Daya Tighaslant; 14. Tessaout; 15. Tizi N'Inouzane; 16. Tigalmamine; 17. Taguelmam n'Harcha; 18. Iguerda-Ait-Amana; 19. Sidi Ali; 20. Dayat Iffir; 21. Dayat Afourgagh; 22. Aït Blal; 23. Aguersif; 24. Col de Zad; 25. Tirsal; 26. Agdal de l'Oukaimeden; 27. Oued Kert; 28. Ifrah; 29. Tissouirine; 30. ODP 976; 31. GeoB 6008-1; 32. Oued Fares (OugartaMountains, Western Sahara, Algeria); 33. KS 78007 (coast of Rabat).

atmospheric humidity is always higher in oceanic situations (Médail & Quézel 1999). Precipitation also increases by about 10% per 100 m of elevation. Mean annual temperature varies between 8 °C and 24 °C, with higher values in a pre-Saharan zone (Tafraoute). Inner areas are characterized by greater continentality, with more extreme variation in daily and monthly temperatures, notably daily values ranging up to 40 °C.

Study species

Argania spinosa is an evergreen tree endemic to the Anti-Atlas/High Atlas Mountains, and the Sahara Desert. It occupies arid and semi-arid areas in southwest Morocco (Fig. 1), dominating the vegetation of ca. 1 million ha (7% of the forested area in the country). Two small populations are reported near Rabat (50 ha) and near Oujda (800 ha) (Msanda et al. 2005), located about 700 and 400 km north of the main range of the species, respectively.

This species is remarkably adapted to aridity, surviving extended drought periods (annual rainfall between 440 mm and 120 mm) and high temperatures (to 50 °C). It occurs in a wide array of soils, ranging from heavy clays to sand dunes, and a broad span of altitudes, from sea level to 1300–1500 m a.s.l. (Msanda et al. 2005). Argan trees play a vital role in maintaining the ecological balance in arid zones because the large root system helps to retain soil, increase fertility and prevent erosion, thereby reducing the impact of desertification and preserving biodiversity (Khallouki et al. 2005).

Faced with desertification from the south and overuse of the land for agriculture, in 1998 Morocco began the preservation of argan tree and designated the Arganeraie Biosphere reserve (UNESCO Man and Biosphere; Charrouf et al. 2002) within the Souss-Massa National Park, previously established in 1991 (Maliha et al. 2008).

Palaeorecords review

To provide a benchmark for the palaeodistribution of argan woodlands in northwest Africa, we reviewed the Quaternary pollen data through the African Pollen Database (http://apd.sedoo.fr/apd/accueil.htm), as well as undertaking a systematic search of the literature (for further details see App. S1). This synthesis encompasses 33 Quaternary marine and continental pollen sequences (see number sites in Fig. 1), but *Argania* cf. *spinosa* pollen was present only at six sites for the Quaternary. Unfortunately, the best known fossil record sequences in continental Morocco do not document the presence of *Argania* pollen.

Species distribution modelling

Argania spinosa records

To estimate the current range and distribution of argan woodlands, we used the forest map of Morocco (1/50000;

Msanda et al. 2005). Specifically, 555 record points were randomly sampled from within the argan woodland polygons, ensuring a minimum distance of 2 km between points in order to reduce spatial autocorrelation. We also randomly took 10,000 background points from throughout the entire study area (i.e. Morocco), including argan woodlands, for both calibration and testing purposes. Wisz & Guisan (2009) have shown that this approach is also valid for the calibration of models that normally need real absence data, e.g. generalized linear models and boosted regression trees.

Climatic variables

The present-day climate was represented by bioclimatic variables (App. S4) in the WorldClim data set (Hijmans et al. 2005) at a 30-s spatial resolution. In order to avoid model overfitting, a subset of six variables were used in calibrating the SDMs (see below). These were selected based on their likely importance for plant species distributions (BIO4 = Temperature Seasonality (SD*100); BIO6 = Minimum Temperature of Coldest Month; BIO10 = Mean Temperature of Warmest Quarter; BIO13 = Precipitation of Wettest Month; BIO15 = Precipitation Seasonality (coefficient of variation); and BIO17 = Precipitation of Driest Quarter), avoiding the inclusion of highly correlated variables. These same six variables were also used to represent the past and future climates.

To represent uncertainty in the palaeoclimatic estimation (Beaumont et al. 2008), we used two general atmospheric circulation models (GCM): the Community Climate System Model (CCSM; https://www2.cesm.ucar.edu/; Kiehl & Gent 2004) and the Model for Interdisciplinary Research on Climate (MIROC, v 3.2; http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dpt_12042129868-625690). The original GCM data were downloaded from the PMIP2 website (http://pmip2.lsce.ipsl.fr/). Then, anomalies between past and present were calculated, statistically downscaled to 30 arc-sec resolution and added to WorldClim current data (http://www.ccafs-climate.org/spatial_downscaling/; Ramirez-Villegas & Jarvis 2010).

During the Last Glacial Maximum (LGM, at 21 ka), ice sheets covered large areas and global temperatures were significantly lower than today (Yokoyama et al. 2000). In the LGM, the Earth's ocean levels were at their lowest point, and extensive reaches of dry land were exposed along the continental coasts. Africa also exhibited a major exposure of continental shelf during the LGM epoch. Recent analyses have suggested a net decrease in eustatic sea level at the LGM ranging from 120 to 135 m (Church et al. 2001; Clark & Mix 2002). Thus, in order to explore the spread of the argan woodlands at LGM, we used these references to derive the reconstruction of coastlines at 21 ka for the study area presented here. Also, the climate of the grid cells exposed at the time of maximum sea level depression was also estimated (Clark & Mix 2002; Huntley et al. 2013).

Future climate was represented by three climate change projections for 2020, 2050 and 2080 (IPPC Third Assessment data) at 30 arc-sec resolution. These data are based on the Canadian Centre for Climate Modelling and Analysis (CCCMA), Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Hadley Centre Coupled Model v 3 (HADCM3) models (Flato et al. 2000; Gordon et al. 2000), and were also directly downloaded from the WorldClim database; for each of the models two emission scenarios (A2a and B2a) reported in the Special Report on Emissions Scenarios (SRES) of the Intergovernmental Panel on Climate Change (IPCC 2007) were used. Each scenario described one possible demographic, politico-economic, social and technological future as expected for 2020, 2050 and 2080. Scenario B2a emphasizes more environmentally conscious and regionalized solutions to economic, social and environmental sustainability. Compared with B2a, scenario A2a also emphasizes regionalized solutions to economic and social development, but it is less environmentally conscious.

Model fitting, hindcasting and forecasting

The current potential distribution of argan was modelled according to the present-day climate. The argan woodland presence data were related to the climatic variables using four different, but widely applied, SDM algorithms: Mahalanobis distance (MH; Farber & Kadmon 2003), generalized linear models (GLM; Guisan et al. 2002), boosted regression trees (BRT; Elith et al. 2008) and Maxent (MX; Phillips et al. 2006). Modelling parameters were those by default, except for the link function (binomial with a logit link) in GLM and the number of trees (2216) and shrinkage (0.01) in BRT, according to a model optimization, which provides the best prediction, minimizing overfitting (i.e. minimize the Bernoulli deviance in both testing and training data sets).

All models were built using a subset of data containing 70% of the sites selected at random. The remaining data (30%) were used to evaluate the predictive performance of the models.

The importance of the individual predictor variables for argan woodland distribution was evaluated based on the two machine-learning procedures, MX and BRT. For MX, we used the built-in Jackknife procedure, and an estimation of the relative influence of each variable in reducing the loss function during the fitting process for BRT.

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Then, in order to study the potential distribution of argan woodland in the past, we used SDM-based hindcasting (Svenning et al. 2011): all the fitted SDM models were applied to the climate data for the LGM and the mid-Holocene. In the same way, we also forecast the potential distribution to future periods (2020, 2050 and 2080), to assess future threats from global warming.

Since the natural origin of the two isolated populations in the north of the study area is controversial, we also built models excluding presence points from these areas, which left a total amount of 542 records of presence. These models were also hindcaste to the LGM and mid-Holocene. Results of this analysis are shown in App. S5a.

To assess whether argan woodlands are currently limited by climate, or also by non-climatic environmental or cultural factors (e.g. over-harvesting and grazing), we compared the current potential distribution with its actual distribution.

To provide binary predictions of suitable areas (presence–absence), we calculated the model-specific thresholds that maximize the sum of sensitivity and specificity (Jiménez-Valverde & Lobo 2007). This method gives the threshold that provides the best compromise between correctly predicted presence values (i.e. sensitivity) and correctly predicted absence values (i.e. specificity). Then, these thresholds were used in all the projections with each respective model.

Final results are shown in the form of ensemble raster maps with values from 0 to 4, which represent the number of models that predict suitability for each pixel in the grid. The GRASS-GIS software (Neteler et al. 2012) was used for all geographic computations on environmental data, as well as to calculate bioclimatic variables. All the models were built, evaluated and projected using the 'dismo' package in R 2.13 (R Foundation for Statistical Computing, Vienna, AT). Additionally, the 'GBM' package and Maxent software (Phillips et al. 2006; http://www.cs.princeton.edu/~schapire/maxent/) were also needed for BRT and for MX, respectively.

Model evaluation

For measures of model accuracy, we provide sensitivity and specificity, as well as the area under the ROC Curve (AUC), Kappa (KAPPA), Pearson's correlation (COR) and the True Skill Statistic (TSS; Allouche et al. 2006). Here, we followed Phillips et al. (2006), who in a novel interpretation of AUC applied it only to presence-based algorithms, stating that "AUC is the probability that a randomly chosen presence site is ranked above a random background site." Additionally, we provided a qualitative validation of the SDM-based hindcasting results by comparing these with the palaeodistribution inferred from the palaeodata synthesis (App. S2).

Results

All SDMs for the current distribution of argan woodlands performed well, with similar high scores for all accuracy measures (Table 1). Notably, the range of AUC was 0.96–0.98 and for TSS was 0.84–0.91.

Climatic forcings on the current range

The MX-based analysis of variable contributions (Table 2) revealed that temperature seasonality (BIO4) – with 46.8% relative contribution – had the highest explanatory power, followed by precipitation of the wettest month (BIO13; 33.4%) and precipitation seasonality (BIO15; 8.5%). Results from BRT model provided similar results, with BIO4 being the most important variable for the distribution of argan woodlands.

According to the MX response curves (Fig. 2), argan woodlands occurred preferentially at low temperature seasonality (BIO4), low minimum temperatures (BIO6), whereas temperature in the warmest quarter (BIO10) was less important. Concerning water availability variables, precipitation of the wettest month (BIO13) showed the strongest discriminant power, reaching maximum values of 30–50 mm. There was also a unimodal response to precipitation seasonality (BIO15), and there was also a weak

Table 1. Accuracy of species distribution models (GLM, generalized linear model; MX, Maxent; MH, Mahalanobis Distance and BRT, Boosted Regression Trees) for the current distribution of *Argania spinosa*.

	T	PREV	SENS	SPEC	PPP	NPP	AUC	COR	KAPPA	TSS
GLM	0.062	0.053	0.94	0.90	0.35	1.00	0.96*	0.62*	0.47	0.84
MX	0.178	0.053	0.95	0.92	0.39	1.00	0.97*	0.65*	0.52	0.87
MH	0.963	0.053	0.97	0.94	0.47	1.00	0.98*	0.52*	0.60	0.91
BRT	0.078	0.053	0.94	0.94	0.45	1.00	0.97*	0.71*	0.58	0.88

T, threshold values that maximized sensitivity and specificity; PREV, prevalence; SENS, sensitivity; SPEC, specificity; PPP, positive predictive power; NPP, negative predictive power; AUC, area under the receiver operator (ROC) curve; COR, Pearson correlation coefficient; KAPPA, Cohen's kappa; TSS, True Skill Statistic; $*P < 0.001$.

Table 2. Relative importance of environmental variables for the current distribution of *Argania spinosa* according to Maxent and Boosted Regression Tree models, represented a heuristic estimate of their relative contributions.

Variables	MX				GBM
	Perc. contribution	Permutation importance	Training gain		Rel. Influence
			Without	With only	
BIO4	46.8	57.8	1.736	0.975	2141.08
BIO13	33.4	22.4	1.714	0.789	1827.78
BIO6	4.4	9.5	1.731	0.307	1331.40
BIO10	4.7	1.6	1.807	0.449	868.79
BIO15	8.5	7.0	1.785	0.473	470.04
BIO17	2.1	1.7	1.816	0.534	563.58
All variables	–	–	1.822	–	–

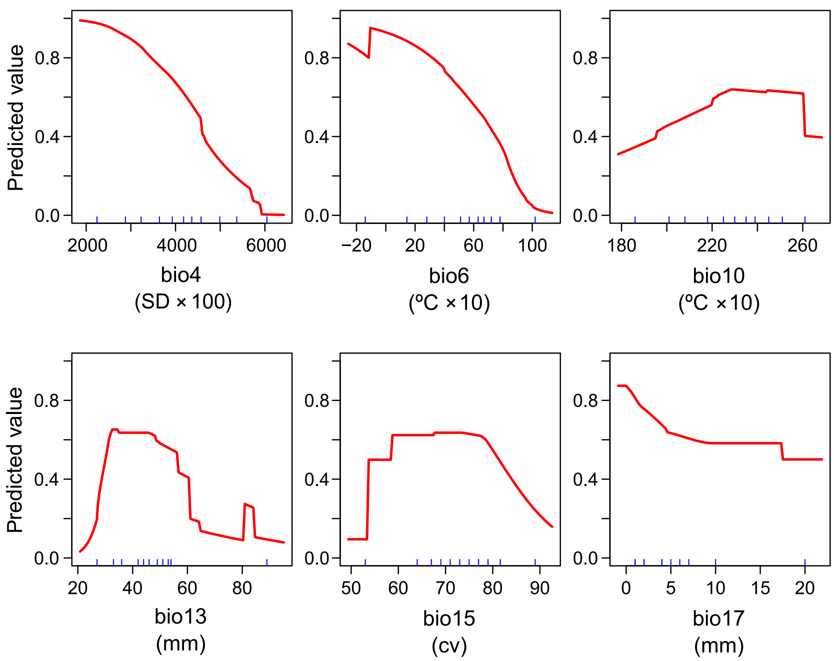

Fig. 2. Response curves of argan woodland distribution for the six bioclimatic variables used in the Maxent model (MX). BIO4 = Temperature Seasonality (SD × 100), BIO6 = Min Temperature of Coldest Month (°C), BIO10 = Mean Temperature of Warmest Quarter (°C), BIO13 = Precipitation of Wettest Month (mm), BIO15 = Precipitation Seasonality (coefficient of variation) and BIO17 = Precipitation of Driest Quarter (mm).

positive trend with decreasing precipitation of the driest quarter (BIO17).

Current argan populations occupy a proportion (~1.0×10^6 ha) of their potential distribution (2.27×10^6 ha predicted for all models), i.e. 44% (Fig. 3, Table 3). Argan woodlands would have been able to grow in most of the adjacent coastal regions (in the neighbourhood of Essaouira, Agadir and Sidi Ifni), and generally on mountain slopes oriented towards the Atlantic Ocean, such as at lower altitudes of High Atlas Mountains in the region of Marrakech. This finding was consistent with previous results (i.e. BIO4 = 46.8% of importance contribution in the Maxent model). In addition, other places where the species could potentially occur are located both south of Sidi Ifni and north of Essaouira, i.e. both at lower and higher latitudes than its current realized distribution.

Late Quaternary shifts in the climatic potential range

The current distribution of argan woodlands does not overlap with its potential refugia at the LGM (under both climate models CCSM and MIROC; Fig. 3). During the full

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Table 3. Size (ha) of the realized distribution of *Argania spinosa* compared to its potential distribution area as estimated with SDMs.

Number of models	Potential area (hectares)	Summed potential area (hectares)	Actual occupied area (hectares)
1	2.247.114	6.043.445	1.032.625
2	800.528	3.796.331	
3	724.076	2.995.803	
4	2.271.727	2.271.727	

glacial, argan woodlands were mostly likely pushed southwards into the current Sahara Desert, extending to the west in exposed shelf areas of the Atlantic coast; and with a northward limit in the Anti-Atlas Mountains. The suitable areas were more fragmented and discontinuous than today, with a tendency to occur at lower altitudes than those they could occupy now or during the mid-Holocene (see Figs 3 and 4).

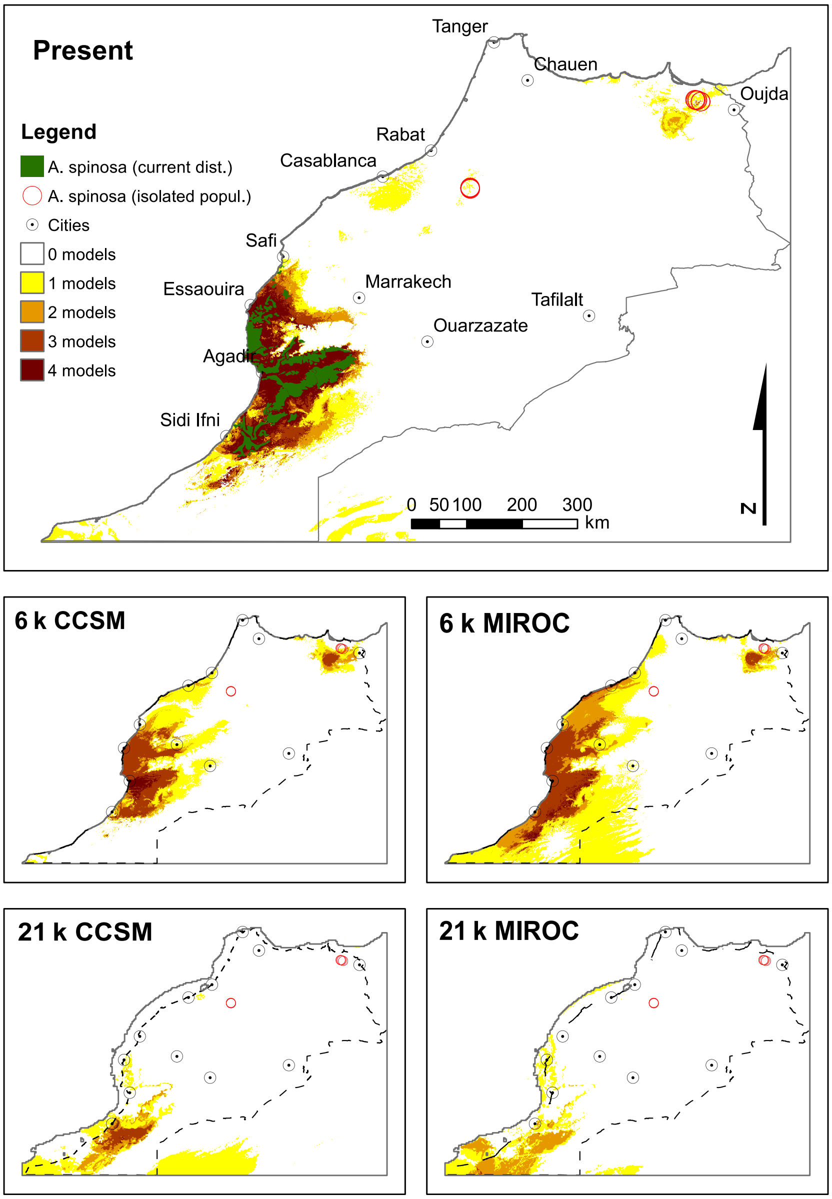

Fig. 3. Potential distribution of Argania spinosa in present and past climate scenarios. The diagrams display the potential range shift during the LGM (emerged shelf areas at this period are shown) and mid-Holocene based on paleoclimatic simulations in two general circulation models (CCSM and MIROC). Green area: currentmain distribution of A. spinosa. Red circles: isolated current populations.

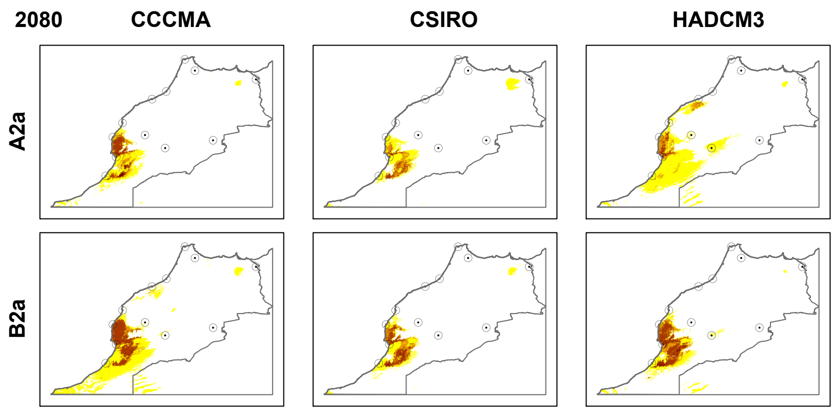

Fig. 4. Predicted potential distribution of Argania spinosa under future climate scenarios for 2080. A2a and B2a SRES scenarios based on simulations of three general circulation models: HADCM3, CSIRO and CCCMA.

Projections for mid-Holocene estimate occupied areas in zones similar to the current distribution (Fig. 3). In particular, there was complete continuity of argan woodland potential distribution area across the Anti-Atlas and High Atlas Mountain system, and a slight tendency for persistence during the mid-Holocene at lower or almost the same altitudes as they occupy now (see Fig. 5). Notably, the MIROC model estimated a wider distribution, extending from areas likely occupied during LGM in the south to more northerly areas than currently occupied.

Following expectations, the highest congruence between models was reached at present, whereas congruence for the mid-Holocene, and especially LGM, suitable areas decreased significantly (App. S6).

The weak support for the present suitability of two northward isolated populations disappears when they are removed from the models (App. S5a), although a relatively large area remained suitable near the population in the Oued Moulouya River. This area appeared suitable in the models for mid-Holocene, but not during LGM.

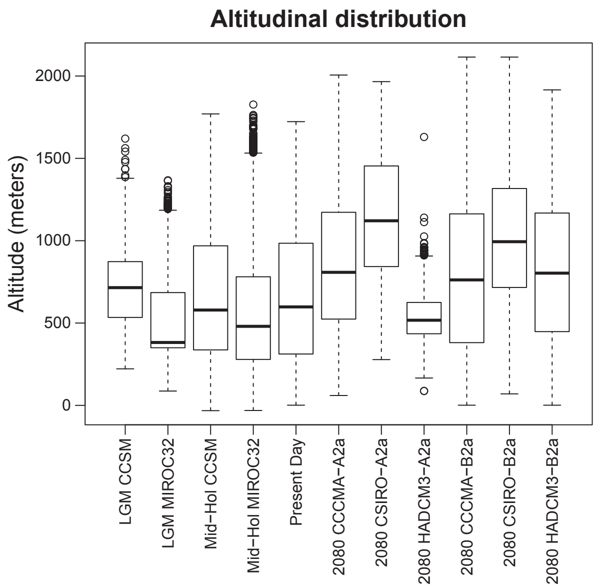

Fig. 5. Altitudinal distribution of suitable areas for *Argania spinosa* during four periods: LGM, mid-Holocene, present-day and 2080; the past periods under two general circulation models (see Fig. 2) and future periods under three general circulation models (see Fig. 3 for climate scenarios).

Future climate change forcings

Projections for the potential argan woodland distribution under future (2080) climate change scenarios indicate that suitable areas may become more limited overall (Fig. 4, App. S5b), with a reduction in the potential distribution of almost 20–30% (App. S6). Remaining and possible future refugia areas include part of the Atlantic coastline, Anti-Atlas Mountains and Souss Valley, despite some differences being found between model projections for different climate change scenarios (CCCMA, CSIRO and HADCM3; for further information see Fig. 4). The southernmost territories near Sidi Ifni appeared likely to cease being suitable, as well as many territories around the Souss Valley (between Agadir and Ouarzazate). Argan could undergo a severe fragmentation and a reduction in Anti-Atlas Mountains and the region between Agadir and Essaouira, where it could maintain its presence along the coastline as well as the on slopes of the High Atlas Mountains, which are oriented towards the sea. The retraction in the potential range was forecasted to intensify as time progresses through the 21st century (App. S6 and S5b). Furthermore, there was a trend for suitable areas for argan woodland to shift to slightly higher altitudes than those occupied today (Fig. 5), with the median altitude for argan woodland potential distribution shifting from 593 m today towards 407–952 m a.s.l. in the future, depending on the climate model and scenario.

Discussion

Our results indicate that climate constrained the distribution of argan woodlands within northwest Africa throughout the Late Quaternary, although non-climatic factors clearly pose an additional constraint on their current distribution. Under global warming, the range of argan woodlands is likely to contract, with no tendency to shift towards northern latitudes and only a slight tendency to shift upwards. Consequently, conservation efforts should be oriented to promoting the *in situ* persistence of this important woodland ecosystem.

Climatic forcing of the current distribution of argan woodlands

Seasonal temperature (BIO4; see Table 2) is the main factor determining the current range of argan woodlands, and it seems that this ecosystem develops primarily under a clear oceanic influence, with frequent fog throughout the year. The low contribution of precipitation during the driest quarter (BIO17) to the models and the relatively flat response curves (Fig. 2) could indicate that the higher humidity of the air masses near the sea would provide enough water for the trees to survive dry periods. Concerning temperature, argan woodlands occur preferentially in areas with relatively cold winters (BIO6) within the region, whereas no strong effect of mean temperature of the warmest quarter (BIO10) was found (Fig. 2). These climate relations correspond to the argan woodland ecosystem's occurrence as part of the Mediterranean–Saharan transition zone (Benabid & Fennane 1994). The strong unimodal response to precipitation of the wettest quarter (BIO13) provides evidence of the argan woodland dependence on a minimum water supply during winters, as well as its absence from the wettest areas (Table 2, Fig. 2). Precipitation seasonality (BIO15) gave a low contribution to the models and a wide response curve. The effect of this variable, as well as the response to precipitation of the driest quarter, corroborates the mediterranean characteristics of argan woodlands.

The fact that argan woodlands do not occupy their entire current potential distribution area suggests that non-climatic factors also play an important role (Figs 1–3, Table 3). Although dispersal limitations could strongly limit the ability of plants to colonize currently suitable areas (Svenning & Skov 2004), given the estimated argan woodland distribution during the LGM, a post-glacial migration lag should cause a more complete range filling near its southern limits and lower range filling in the north. This pattern was not detected in our data. Hence, we propose that human pressure could be a more feasible explanation (App. S1). Pollen sequences indicate that argan woodlands, at least during the late Holocene, had a larger and continuous distribution throughout the Atlantic coast of Morocco (see Cape Ghir sequence (#31) for the past 2000 yr; McGregor et al. 2009). However, human activities during several millennia have led to argan woodland losses (e.g. Jalut et al. 2009). Severe deforestation has been documented to have occurred since the 18th century (Nouaim et al. 1991), when dense argan woodlands reportedly covered a much larger area than today, suggesting a boundary contraction of 200 km at both northern and southern limits (Msanda et al. 2005). At the end of 20th century the argan woodland range had fallen below 6 million ha (Ellatifi 2005), with an estimated deforestation rate of 600 $ha \cdot yr^{-1}$ (Majourhat et al. 2007). The most vulnerable area is at the southern limit, where the argan woodland ecosystem during the last century lost half of its surface area as a result of overgrazing, deforestation and extreme water stress (Tarrier & Benzyane 2003).

Past climatic forcings on the distribution of argan woodlands

It is well known that tree flora in North Africa has undergone major range shifts due to the Quaternary climate changes (e.g. Cheddadi et al. 2005). Our results support the contention that argan woodlands were also strongly affected. During the LGM argan woodlands could have extended southwards into the current Sahara Desert. During the warm and relatively moist mid-Holocene, argan woodlands could have expanded towards northern and inner areas of Morocco. The progressive shift in the potential range of these woodlands during the late Quaternary reflects the estimated marked climate sensitivity of this ecosystem. These findings are consistent with the phylogeography and palaeobotanic record for *A. spinosa* (see below).

Last Glacial Maximum

Our results suggest that the LGM climate should have provoked a strong shift in argan woodland distribution. These findings are supported by the palaeodata (see palaeodata synthesis in App. S1) and previous phylogeographic studies (El Mousadik & Petit 1996a,b; Petit et al. 1998). Additionally, our results suggest that during the last glacial the argan woodlands could have extended southwards into the current Sahara Desert, in disagreement with earlier hypotheses (Benabid 1985).

Notably, our findings imply that the two isolated northern populations (Beni-Snassen in northeast of Oujda and

Oued Grou southeast of Rabat; Fig. 1) are not relicts of a previously widespread distribution during the last glacial. Phylogeographic studies have suggested seed transfer by humans from the main range as a more plausible interpretation (El Mousadik & Petit 1996a). Argan pollen from the late Holocene (ca. 3 ka before present, but never earlier) in the Eastern Moroccan Rif (site #27; Barathon et al. 2000) supports the idea that this disjunctive population was introduced by humans. Similar findings have been identified in Australia (Kondo et al. 2012). Furthermore, argan pollen is absent from a deep-sea core (site # 33) near the coasts of Rabat as well as in two lagoon ecosystems (sites #9 and #12) close to the second disconnected population, implying that the argan tree was likely not distributed in northwest Morocco between the LGM and 3 ka before present.

Our modelling for the LGM shows that argan woodlands could have extended southwards, with a southernmost distribution limit at the current Sahara Desert. Findings of argan pollen from the Western Sahara in the Alborán Sea (site # 30; further details in App. S1) from the last glacial support this finding. These areas could be suitable for argan woodland because of higher rainfall than today (App. S3, S7). Indeed, the maximum suitable area for argan woodlands could have been in an intermediate position between the distant sea ice cover and the glaciers of the High Atlas Mountains and Middle Atlas Mountains (Fig. 1), i.e. both in subcoastal areas (Souss Valley) as well as southward latitudes (western Sahara). Earlier studies provide evidence that the southern Maghreb and the northern Sahara were cooler during the LGM, but not continuously dry (Rognon 1987), supporting the palaeoclimate reconstructions. Furthermore, pollen fossil data clearly show that the Moroccan landscape at the LGM was dominated by steppe vegetation, with patches of trees at certain sites in the Atlas Mountains (Rhoujjati et al. 2010). Unfortunately, the only *in situ* evidence of *Argania* pollen beyond its southernmost distribution limit comes from the Ougarta Mountains in the Algeria desert (see Fig. 1; site #32), dated to sometime in the Pleistocene (Beucher 1967).

Mid-Holocene

For the mid-Holocene, agreement between SDM algorithms strongly supports a northward range shift of argan woodlands since the LGM (Fig. 3). After the LGM, a warmer and more humid period succeeded from 14.5 ka to 6 ka, named the Holocene African Humid Period (HAHP; COHMAP Members 1988). It seems likely that an argan expansion, as for other vegetation tolerant to water stress (xerophytic woods/scrub and tropical dry forest) could have occurred towards both northern and inner areas of the Souss Valley. Palaeodata support far moister conditions in the Sahara region during the HAHP (Wickens 1984), when the Saharan mountains supported woodland or scrub, including typically Mediterranean taxa until 6 ka (Jolly et al. 1998). The northward shift of the argan population is reflected in high argan pollen percentages (*ca.* 7%) recorded in a Holocene sequence from the Tissouirine snailery (# 29; early Neolithic ca. 6 ka). However, this northward spread did not reach the Rif Mountains despite this area being suitable according to our estimates, as indicated by the absence of argan pollen at sites # 9, 11, 12 and 33. In addition, a moderate uphill shift in response to the increasing temperature was predicted in our models (Fig. 5). Pollen findings near Ouarzazate (site # 13) could provide evidence of upper and easternmost limits for argan past distribution.

Subsequently, the climate changed towards more arid conditions from ca. 6 to 4 kyr ago (Drake & Bristow 2006; Holmes 2008). There is disagreement about the abruptness of mid-Holocene aridification in North Africa, with evidence indicating both abrupt vegetation collapse as well as gradual vegetation decline (e.g. Liu et al. 2007). This could be in line with the discrepancies between the two climatic models (CCSM and MIROC). The warming and desiccation (see App. S3, S7) of the Western Sahara region since the mid-Holocene have led to a sharp decline of forested areas in previous humid stages. No evidence of human activity was detected (Chennaoui et al. 2005). Indeed, the potential distribution of argan woodlands was estimated from our modelling to have retracted northwards during this period (Fig. 3).

Threats of global warming and future potential distribution

The climate sensitivity of the argan woodland ecosystem, as well as the impact of human pressure, are likely responsible for its currently low range filling, and should be taken into account for future management and conservation.

Although tree species could shift to northern latitudes and higher altitudes in response to climate changes (Parmesan & Yohe 2003), our results (Fig. 5, App. S5b) suggest a marked decline/contraction of the argan potential distribution instead of a strong latitudinal shift. The predicted future contraction is particularly severe for the southernmost argan woodlands, probably reflecting a more pronounced aridity trend (Fig. 4) in the area next to the Sahara Desert. Even if argan finds suitable areas beyond its current range, the expected climate changes are rapid and may even occur abruptly (Alley et al. 2003). In either case, they would be expected to be faster than what can reasonably be expected in terms of tree migration rates (Iverson et al. 2008). Additionally, strong delays in ecosystem development should be expected (Svenning & Sandel

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2013), with likely strong consequences for the ecosystem services provided.

Regarding the predicted slight altitudinal shift, a moderate rise in altitude is expected in those populations located near the mountains (Figs 4 and 5; e.g. Svenning & Skov 2007a,b), but in the case of argan woodlands, most of the populations probably will not progress upwards. According to our models based on climatic variables, the trees will remain in an intermediate position in order to avoid the heat and also to receive moisture from the ocean (Table 2; see models contribution of BIO4). In fact, recent studies (Crimmins et al. 2011) demonstrated that climate change during the 20th century has resulted in a significant downward shift due to the climatic water balance rather than temperature increases.

Given our climate-based forecasts, a key factor for the future status of the argan woodland ecosystem will be its ability to persist in its current locations, suggesting that efforts should be made to maintain established argan stands, preventing overgrazing and deforestation caused by charcoal production and clearance for crop fields (Belyazid 2000). This will be a particular challenge because the future suitable areas for argan woodlands coincide with regions of high human pressure (Médail & Diadema 2009). Specifically, the Arganeraie Biosphere reserve supports ca. 3 million inhabitants (Bridgewater 2002), but argan has not yet been assessed for the IUCN Red List. The human threat, however, comes not only from the degradation and destruction of established argan woodlands (Belyazid 2000), but may also come from the limit to colonization of potentially new areas near Atlantic coastline because of decreasing migration rates (Collingham & Huntley 2000).

Conclusions

The case of the argan woodland ecosystem highlights the importance of using SDM in conjunction with the available pollen fossil evidence in order to gain a better understanding of an ecosystem's climate sensitivity and associated long-term range shifts, as well as for disentangling climate and non-climate effects on plant distributions.

Judging by the results found here, the glacial–interglacial climate changes have forced major shifts in the range of argan woodlands during pre-anthropic stages. Even the distribution models support the hypothesis of an argan distribution during the LGM at more southern latitudes, into the current Sahara Desert. During the Holocene a subsequent expansion and later contraction of the range of argan woodlands may have occurred in response to the Holocene climate development, with an increasing interaction with human impact. The strong desertification that has occurred since the mid-Holocene at the southern limit of the current argan woodland range is thus most likely the outcome of a combination of both climatic and anthropic pressure. Consequently, if the past potential ranges reflect reality, then implications for argan trees are far-reaching for the future. Facing global warming, argan populations could be expected to shift their range northwards and uphill, although under future scenarios these woodlands will be unlikely to find suitable areas at northern latitudes or higher altitudes.

In view of the climate-based predictions and the important role of argan woodlands in preventing desertification and maintaining the local social and economic systems dependent on this key ecosystem, vigorous efforts should be made to protect all currently established argan woodlands.

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Author contributions

F.A.S. and J.A.L.S. conceived the ideas; F.A.S. and J.A.L.S. collected the material; F.A.S. designed the experiments; FAS and D.N.L. analysed the data; J.C.S. contributed to discussion of the results; F.A.S. and J.A.L.S wrote the paper and D.N.L and J.C.S. commented on drafts of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Paleobiogeography and Paleodata synthesis.

Appendix S2. Model accuracy and prediction uncertainty.

Appendix S3. Climate scenarios for Morocco.

Appendix S4. Predictor variables included in the models and current distribution of argan woodlands (green).

Appendix S5. (a) Potential distribution of *Argania spinosa* in present and paleoclimate scenarios when the two isolated populations (red circles) were removed from the presence data set in the model-building processes – LGM (exposed shelf areas are shown) and Middle Holocene under two general circulation model estimates (CCSM and MIROC); (b) Predicted potential distribution areas for *A. spinosa* in future periods (2020 and 2050).

Appendix S6. Argan potential area (ha) estimated by SDMs (GLM, Maxent, Mahalanobis and Boosted Regression Trees) in the different climate scenarios.

Appendix S7. Boxplots representing both (a) annual temperature (Tann) and (b) annual precipitation (Pann) in the different climate scenarios.

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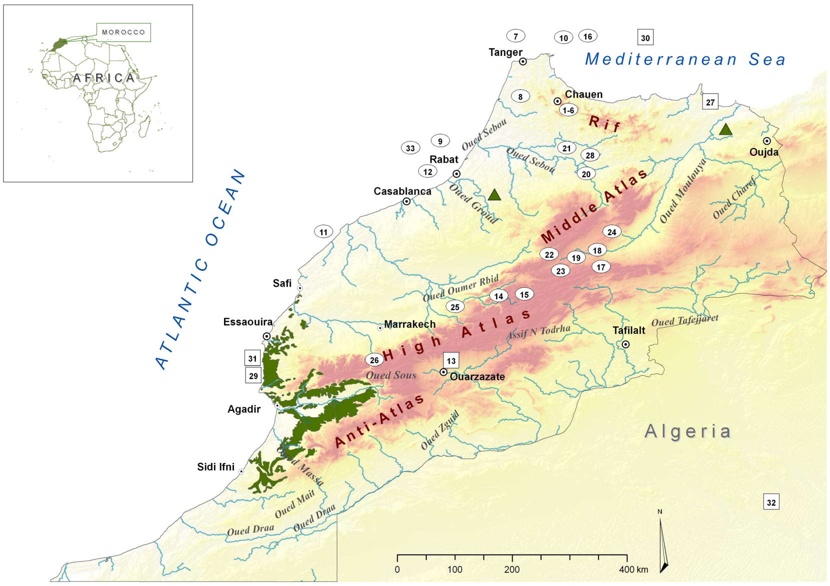
Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.



North African dry woodlands constitute Mediterranean climatic-ecotone ecosystems of vital importance for human livelihoods and local biodiversity. To improve the basis for managing these key ecosystems, we have selected a Tertiary relict woodland (*Argania spinosa*) in order to clarify the sensitivity to long-term climate change (the present, the past glacial-interglacial cycle, and under future scenarios).