

Climatic forcings on past and future range dynamics of the argan (*Argania spinosa*) woodland ecosystem in North Africa

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ABSTRACT

Aim Argan (*Argania spinosa*) woodland constitutes a Mediterranean climatic-ecotone ecosystem of vital importance for human livelihoods and local biodiversity in northern Africa. In order to improve the basis for managing this key Mediterranean ecosystem, we aim to clarify its sensitivity to climate change during the present, the past glacial-interglacial cycle, and under future climate change scenarios. We also discuss the importance of human land-use for distribution of argan woodlands.

Location Morocco and Western Sahara (Northern 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 years ago) and Mid-Holocene (6,000 years ago) – the coldest and warmest periods during the last 100,000 years. Model predictions for past scenarios were compared with Quaternary paleorecords to evaluate their accuracy. Finally, we forecasted changes in the potential range to year 2080 to assess its likely future range dynamics.

Results During 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 similar areas as today. The estimated past distributions are consistent with paleorecords of *A. spinosa*, providing evidence for the important role of Quaternary climate changes in driving argan woodland range dynamics. Currently, range filling constitutes 44 % of the potential distribution, probably primarily reflecting anthropic land-use effects. Future climate change is forecasted to not cause latitudinal or altitudinal range shifts, but rather an overall range contraction.

Main conclusions The argan woodland ecosystem shows high climatic sensitivity. Notably, strong range shifts are estimated in response to past climate changes, in agreement with paleorecords. The estimated climatic sensitivity also predicts severe

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range contraction during future climate change. In consequence, management strategies for these woodlands should be developed to facilitate their in-situ survival, notably by reducing the currently intensive human pressure.

Keywords: Morocco, Palaeobiogeography, Pollen fossil records, Quaternary Climate Change, Sapotaceae, Species Distribution Modeling, Western Sahara

INTRODUCTION

A global overview reveals that warming and decreased water supplies are the main risk factors for tree losses and forest die-back (Allen *et al.* 2010). Drought-induced tree mortality have 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 impacts may be particularly drastic in areas already subject to a high degree of aridity stress, and water is the most important limiting resource (Peñuelas and Boada, 2003). Dryland forests account for 6% of the world’s forests and provide key ecosystems for human livelihoods to over one billion 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 attention by the scientific community (López-Sáez & Alba-Sánchez, 2009), despite its importance for biodiversity conservation as well as human livelihoods.

North African dryland forests, part of the Mediterranean biogeographic region, is already facing the consequences of ongoing climate change (climate warming and water stress), as well as intensive 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 “phylogeographical 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 an endemic ecosystem for the Western Mediterranean region (south-western Morocco) at the edge of the Sahara Desert (Bani-Aameur *et al.*, 1999). Argan woodlands are still relatively extensive, but rapidly declining as a result of anthropic disturbance (overgrazing, deforestation) and climatic stress (droughts, desertification) (Tarrier and 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 (López-Sáez and Alba-Sánchez, 2009; Le Polain de Waroux and 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).

Currently, *A. spinosa* is the only representative of the amphi-Atlantic tropical/subtropical family Sapotaceae in northwestern Africa (Pennington, 1991). The clade Sideroxyloae (including *Argania*, *Sideroxylon* L. and *Nesoluma* Baill.) presents extensive ecological variation and a highly disjunct distribution (Africa including Macaronesia, the Americas, and islands in the Indian Ocean), reflecting its past continuous range across the Northern Hemisphere during the early Tertiary (Smedmark & Anderberg, 2007) and a subsequent contraction towards the equator (Collinson *et al.*, 1981) around the Eocene/Oligocene boundary (*c.* 34 Ma). *A. spinosa* hence could be considered a Mediterranean Tertiary relict tree, given both its evolutionary singularity

(Msanda *et al.*, 2005) and its geographical rarity. It furthermore has high habitat specificity (REF), perhaps reflecting its evolutionary adaptation to semiarid environments.

Because 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 counter-act their future risk exposure. Here, we assess the possible shifts of argan woodlands in North Africa since the Last Glacial Maximum, Based on a review of the Quaternary fossil evidence for the distribution of *A. spinosa* as well as preceding studies on argan populations' genetic structure (El Mousadik & Petit, 1996a and 1996b; Petit *et al.*, 1998), we hypothesize the range of this species extended to more southern latitudes than at present during the LGM episode. Additionally, we critically assessed the argan range in northern Morocco as previous studies suggested (Benabid, 1985), at least during the Late Quaternary.

Using Species Distribution Modelling (SDM) we aim to: i) determine which current climatic factors limit the present-day distribution of argan woodlands; ii) assess the impacts of late Quaternary climate change (Last Glacial Maximum, LGM, *c.* 21 ka, and mid-Holocene, *c.* 6 ka) on its past potential distribution in combination with pollen fossil sequences; and iii) determine the likely consequences of future climate change for this ecosystem.

MATERIALS AND METHODS

Study area

Morocco is situated in the Western Mediterranean region, on the extreme north-western of Africa and is bordered by Mauritania and Algeria, extending from 28° to 36°N and from 2° to 12°W. 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 separates 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 characterises the Moroccan climate. Precipitation decreases while the temperature increases from north to south and from west to east (Le Houérou, 1986). In the north, rainfall varies between 800 and 2000 mm, reaching maximum values on the north-west Atlantic Coast; while at the edge of western Sahara precipitation is as low as 100-400 mm. In addition, atmospheric humidity is always higher in oceanic situations (Médail & Quézel, 1999). Precipitation also increases with about 10% per 100 m of elevation. Mean annual temperature varies between 8 and 24°C, with higher values in a pre-Saharan zone (29.2°C in Tafraoute). Inner areas are characterized by greater continentality, with more extreme variation in daily and monthly temperatures; notably daily values may range 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 semiarid areas in south-western Morocco (Fig. 1) where it dominates vegetation in c. 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 temperature (until 50°C). It occurs in a wide array of soils, ranging from heavy clays to sand dunes, and broad span of altitudes, from sea level to 1300-1500 m (Msanda *et al.*, 2005). Argan trees play a vital role in maintaining the ecological balance in arid zones because their large root network helps to retain soil, increase the fertility, prevent the erosion, reducing the impact of desertification and preserving the biodiversity (López Sáez & Alba Sánchez, 2009).

Species Distribution Modelling

Argania spinosa records

The forest map of Western Anti-Atlas (Morocco) was used as the cartographic base to estimate the current range of argan woodlands (Msanda *et al.*, 2005). In total, 555 records of argan woodlands were randomly sampled from the argan woodland polygons, ensuring a minimum distance between points of 2 km in order to reduce spatial autocorrelation effects. We also used 10,000 background points, selected randomly from across the whole study area, including argan woodlands. We used the background data for both calibration and testing purposes. Wisz & Guisan (2009) has shown that this approach is valid also for the calibration of those models that normally need real absence data, e.g., Generalized Linear Models and Boosted Regression Trees. Additionally, we provided an overview of the past distribution of argan woodlands and a qualitative validation of the SDM-based hindcasting results by reviewing the Quaternary pollen data available in Morocco (see number sites in Fig. 1 and the Paleobiogeography and Paleodata synthesis in Supplementary Information for further details).

Climatic and physiographic variables

Present-day climate was represented by bioclimatic variables in the WorldClim data set (Hijmans *et al.*, 2005) at 30 seconds spatial resolution. In order to avoid model overfitting and, thus, the estimated climatic niche, a subset of six variables were used as predictors in the SDM calibration (see below). These were selected based on their likely importance for plant species distributions (BIO4 = Temperature Seasonality (standard deviation*100); BIO6 = Min 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.

Paleoclimate data for the coldest period (LGM, 21,000 years ago) and the warmest period Mid-Holocene (6,000 years ago) within the last glacial-interglacial cycle also came from WorldClim. We used estimates based on two general atmospheric circulation models (GCM) in order to represent uncertainty in the paleoclimatic estimation (Beaumont *et al.*, 2008): the Community Climate System Model [CCSM,

<http://www.cesm.ucar.edu/>] (Kiehl & Gent, 2004) and the Model for Interdisciplinary Research on Climate [MIROC, ver. 3.2; <http://www.ccsr.u-tokyo.ac.jp/ehhtml/etopindex.shtml>]. The Worldclim paleoclimate data were derived from the original GCM data by statistically downscaling to 30 arcsec resolution (REF). Africa exhibits an important exposure of continental shelf during the LGM epoch. In order to explore the past spread of the argan woodlands, the climate of the grid cells exposed at the time of maximum sea-level depression is also shown.

Future climate was represented by three climate change projections for 2020, 2050 and 2080 (IPCC 3rd Assessment data), based on the Canadian Centre for Climate Modelling and Analysis (CCCMA), Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Hadley Centre Coupled Model version 3 (HADCM3) models (Flato *et al.*, 2000; Gordon *et al.*, 2000); for each of the models two emission scenarios (A2a and B2a) reported in the Special Report on Emissions Scenarios (SRES) by the Intergovernmental Panel on Climate Change (IPCC, 2007) were used as well.

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 (2.216) and shrinkage (0.01) in BRT.

All models were built using a subset of data containing 80% of the sites selected at random. The remaining data (20%) was 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 the two machine-learning procedures, MX and BRT, using the built-in Jackknife procedure for MX and an estimator of the relative influence of each variable in reducing the loss function during the fitting process for BRT.

Then, in order to study the potential distribution of argan woodland in the past, we used SDM-based hind-casting (REF): all the fitted SDM models were applied to climate data for the Last Glacial Maximum (LGM, *c.* 21 ka) and the middle Holocene (mid-Holocene, *c.* 6 ka) with slightly higher temperatures than present (see Fig. S1) or just higher winter temperatures than present. In the same way, we also forecasted the potential distribution to future periods (2020, 2050, and 2080), to assess future threats from global warming.

Since the natural origin of two isolated populations in the north of the studied area is controversial, we also build models excluding presence points from these areas, which left a total amount of 542 records of presence. These models were also hind-casted to the LGM and mid-Holocene. Results of this analysis are shown in Supplementary Information (Fig-S3).

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

In order to provide binary predictions of suitable areas (presence-absence) we calculated the thresholds which maximize sensitivity (i.e., the percentage of presence correctly predicted) and specificity (i.e., the percentage of absence correctly predicted) for each model (Jiménez-Valverde & Lobo, 2007), and then used these in all projections with the respective model.

Final results are shown in form of stack raster map 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 (GRASS Development Team, 2008) was used to all geographical computations on environmental data, as well as climatic data standardization and bioclimatic calculations. We built, evaluated and projected all models using the “dismo” package in the R statistical environment 2.13 (R Development Core Team, 2007). For BRT model the “GBM” packages were also needed.

Model evaluation

As 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). Phillips *et al.* (2006), in a novel interpretation of AUC applied only to presence-based algorithms, state that ‘AUC is the probability that a randomly chosen presence site is ranked above a random background site’. AUC was interpreted as follow: AUC near 0.5 are similar to random prediction and indicate poor model performance, AUC above 0.9 indicate excellent model performance.

RESULTS

All SDMs for the current distribution of argan woodlands showed good performance, with similar high scores for all accuracy measures (Table 1). Notably, AUC ranged 0.98-0.99 and TSS 0.93-0.96.

Climatic forcings on the current range

The MX-based analysis of variable contributions (Table 2) revealed that temperature seasonality (BIO4) —with 53% relative contribution— had the highest explanatory power followed by precipitation of the wettest month (BIO13) (29%), and precipitation seasonality (BIO15) (7%). Results from GBM model provided similar results, with BIO4 being the most important variable for the distribution of argan woodlands.

According to the MX response curves (Fig 3) argan woodland 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 at 30-50 mm. There was also a unimodal response to precipitation seasonality (BIO15), and there was also a weak positive trend with decreasing precipitation of the driest quarter (BIO17).

Current argan populations occupy only a small proportion ($\sim 1.0 \times 10^6$ hectares) of their potential distribution (2.37×10^6 hectares predicted for all models), i.e., 44 % (Fig. 2 and 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 toward the Atlantic Ocean, such as at lower altitudes of High Atlas Mountains in the region of Marrakech. This finding was consistent with the results previously presented (i.e. BIO4=53.0 % of importance contribution in the Maxent model). In addition, other places where the species could potentially occur are located both southern of Sidi Ifni and northern of Essaouira, e.g., 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. 2). During the full 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 at today, with a tendency to occur at lower altitudes than those they could occupy now or during the mid-Holocene (see Fig. 2, 4).

Projections for mid-Holocene estimate occupied areas in similar areas as the current distribution (Fig. 2). In particular, there was complete continuity of argan woodlands' 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). Interestingly, 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, in LGM suitable areas decreased significantly (Fig. S4).

The weak support for the present suitability of two northward isolated populations disappears when they are removed from the models (see Fig. S3), although a relatively large area remained suitable near the population in the Oued Moulouya River. This area appeared suitable already in the models for mid-Holocene, but not during LGM.

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 and S5), with a reduction in the potential distribution of almost 20-30 % (Fig. S4). Possible future refugia areas include part of the Atlantic coastline, Anti-Atlas Mountains, and Sous Valley, despite some differences between model projections for climate change scenarios (CCCMA, CSIRO and HADCM3; for further information see Fig. 4) were observed. The most southern territories near Sidi Ifni appeared likely to cease being suitable, as well many territories around the Sous Valley. Argan could experience a severe fragmentation and a reduction in Anti-Atlas Mountain and the region between Agadir and Essaouira, where it could maintain in the coastal line as well as the slopes of the High-Atlas Mountain which are oriented to the sea. The decrease in the potential range was estimated to intensify as time progresses across the 21st century (Fig. S4-S5). Furthermore, there was a tendency for suitable areas for argan woodland to shift to slightly higher altitudes than occupied today (Figs. 4 and 5), with the median

altitude for argan woodlands located at 593 m today, but occurring at altitudes ranging between 407-952 m.a.s.l. in the future.

DISCUSSION

Our results indicate that climate has constrained the distribution of argan woodlands within north-western Africa throughout the Late Quaternary, although non-climatic factors clearly pose an additional constraint on their current realized distribution. Under global warming, the range of argan woodlands is likely contract, with no tendency for a shift towards northern latitudes and only a slight upward shift. In consequence, it will be critical for the conservation of this important woodlands ecosystem that efforts are implemented to promote its persistence in situ.

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 primarily develops under a clear oceanic influence, with frequent fog throughout the year. The low contribution of precipitation of the driest quarter (BIO17) to the models and the relative flat response curves (Fig. 3) could indicate that the higher humidity of the air masses near the sea would provide water enough to overcome dry periods. Concerning temperature, argan woodlands occur preferentially in areas with relatively cold winters (BIO6) within the region whereas there was no strong effect of mean temperature of warmest quarter (BIO10) (Fig. 3). 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 wettest quarter (BIO13) provide evidence the argan woodlands' dependence on a minimum water supply during winters as well as absence from the wettest areas (Table 2 and Fig. 3). Despite precipitation seasonality (BIO15) shows a low contribution to the models and their wide response curve, when taken into account with precipitation of wettest quarter it evidence the Mediterranean character of argan woodlands.

The moderate range filling of current potential distribution suggests that non-climatic factors also play an important role (Figs.1-2, Table 3). Although dispersal limitations could strongly limit the ability of plants to colonize areas currently suited to them (Svenning & Skov, 2004), given the estimated argan woodland distribution during the LGM a postglacial migrational lag should cause a more complete range filling near its southern limits and lower range filling in the north. This pattern was not observed in our data. Hence, we propose that human pressures could be a more feasible explanation (see Supplementary Information). Pollen sequences indicate that at least during the late Holocene argan woodlands had a larger and continuous distribution throughout the Atlantic coast of Morocco [see Cape Ghir sequence (#31) for the past 2000 years (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 woodland were observed across much bigger areas 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/year (Majourhat *et al.*, 2007). The most vulnerable area is at the southern limit, where the argan woodland

ecosystem during ... has lost half of its surface area as 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 strong range changes due to the Quaternary climate changes (e.g. Cheddadi *et al.*, 2005). Our results support 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 shifts in the potential range of these woodlands during the late Quaternary reflects the estimated high climate sensitivity of this ecosystem. These findings are consistent with the phylogeography and paleobotanical record for *A. spinosa* (see below).

Last Glacial Maximum

Our results suggest that the LGM climate should have elicited strong shift in the argan woodland distribution. This finding is supported by the paleodata (see...) and previous phylogeographic studies (El Mousadik & Petit, 1996a and 1996b; Petit *et al.*, 1998) and the hypothesised range shift southward, but not a wider distribution in whole Morocco (Benabid, 1985).

Notably, our findings suggest that the two northward isolated populations (Beni-Snassen in north-east of Oujda, and Oued Grou south-east 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 (REF). Argan pollen from the late Holocene (*c.* 3 ka before present, but never earlier) in the Eastern Moroccan Rif (site #27; Barathon *et al.*, 2000) support the idea that this disjunctive population is an anthropogenic introduction. 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, which suggest that the argan tree was likely not distributed in northwest Morocco between the Last Glacial Maximum and 3 ka before present.

Our modelling for the LGM show that argan woodlands could have extended southwards, with a southernmost distribution limit with the current Sahara Desert. Findings of argan pollen from Western Sahara in Alborán Sea (site # 30; further details in Supplementary Information) from the last glacial support this finding. These areas could be suitable for argan woodland because of higher rainfall than today (see Figs. S1 and S2). Indeed, the maximum suitable area for argan woodlands could have been in an intermediate position between the faraway-sea-ice cover and the glaciers of High Atlas Mountains and Middle Atlas Mountains (Fig.1), i.e., both in subcoastal areas (Sous Valley) as well as southward latitudes (Western Sahara). Earlier studies provide evidence that the South Maghreb and the northern Sahara were cooler during the LGM, but not continuously dry or not drier as expected (Rognon, 1987), supporting the paleoclimate reconstructions. Furthermore, pollen fossil data clearly show that the Moroccan landscape at LGM was dominated by steppe vegetation with patches of trees in certain sites in the Atlas Mountains (Rhoujjati *et al.*, 2010). Unfortunately, the only *in situ* evidence of *Argania* pollen at its southernmost distribution limit comes from

Ougarta Mountains in 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 the potential range for argan woodlands since the LGM (Fig.2). 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 moisture-demanding biomes (xerophytic woods/scrub, and tropical dry forest) could have occurred towards both northern and inner areas of the Sous Valley. Paleodata supports 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 shift northward of argan population is supported by high argan pollen percentages (*c.* 7%) recorded in a Holocene sequence from the Tissourine snailery (# 29) (early Neolithic; *c.* 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 in sites # 9, 11, 12, 33. In addition, a moderate uphill shift in response to the increasing temperature was predicted by our modelling (Fig. 5). Pollen findings near Ouarzazate (site # 13) could evidence the upper and easternmost limits for argan distribution.

Subsequently, a climate change toward more arid conditions happened since *c.* 6-4 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 Figs. S1-S2) of the Western Sahara region since the mid-Holocene have led to a sharp decline of forested areas in previous humid stages, with no evidences of human impact in this deforestation (Chennaoui *et al.*, 2005). Indeed, the potential distribution of argan woodlands was estimated to have retracted northward during this period by our modelling (Fig. 2).

Threats of global warming and future potential distribution

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

Although tree species could shift to northern latitudes and higher altitudes as response to climate changes (Parmesan & Yohe, 2003), our results (Figs. 4-S5) suggest a strong decline/contraction of the argan potential distribution instead of a strong latitudinal shift. The predicted future contraction is particularly strong for the southernmost argan woodlands, probably reflecting a stronger aridity trend (Fig. 4) in the area next to the Sahara Desert. Even if argan would find suitable areas beyond its current range, the expected climate changes are fast 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 must be expected (Svenning & Sandel, 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. 2 and 4; e.g. Svenning & Skov, 2007a, 2007b), but in the case of argan woodlands most of the populations probably will not go up. They will remain in an intermediate position in order to avoid heating and also 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 20th century has resulted in a significant downward shift due to climatic water balance rather than temperature increase.

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 woodlands, preventing overgrazing and deforestation due charcoal production and clearance for crop fields (Belyazid, 2000). This will be a particular challenge as the future suitable areas for argan woodlands coincide with regions of high human pressure (Médail & Diadema, 2009). The human threat, however, does not only come from the degradation and destruction of established argan woodlands (Belyazid, 2000), but may also limit colonization of potentially new areas near Atlantic coastline by 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 evidences 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 distributions.

Judging by the results obtained, the glacial-interglacial climate changes have forced important shifts in the range of argan woodlands during pre-anthropogenic 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 impacts. The strong desertification that has occurred since the mid-Holocene at the southern limit of the current argan woodland range is thus mostly like the outcome of a combination of both climatic as anthropic pressures. Consequently, if the past potential ranges reflect what in reality happened, then implications for argan tree are far-reaching in the future. Facing the global warming, argan populations could be expected to shift their ranges northwards and up-hill, however under future scenarios it likely will not find suitable areas at northern latitudes neither higher altitudes.

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

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FIGURES AND TABLES

Figure 1 Geographical distribution of *Argania spinosa* (main range: green shape; isolated population: green triangles) in Morocco. Location of Quaternary pollen records (squares indicate the records with presence of argan pollen/oval figures, not presence): 1. Daya Arbatète; 2. Bab Taza/Fifi; 3. Marzine; 4. Tanakob; 5. Bou-Hachem; 6. Jbel Tizirène; 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 Farès (Ougarta Mountains, Western Sahara, Algeria); 33. KS 78007 (coast of Rabat).

Figure 2 Potential distribution of *Argania spinosa* in present and past climate scenarios. The diagrams display the potential range shift during the LGM (exposed shelf areas are shown) and mid-Holocene based on paleoclimatic simulations in two general circulation models (CCSM and MIROC). Green area: current main distribution of *A. spinosa*. Red circles: isolated current populations.

Figure 3 Response curves of argan woodland distribution for the six bioclimatic variables used in the maxent model.

Figure 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.

Figure 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. 4 for climate scenarios).

Table 1 Accuracy of species distribution models (Generalized Linear Model –GLM–, Maxent –MX–, Mahalanobis Distance –MH– and Boosted Regression Trees –BRT–) for the current distribution of *Argania spinosa*.

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

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

SUPPLEMENTARY INFORMATION

Paleobiogeography and Paleodata synthesis

Sapotaceae are an important component of rain forests in all tropical regions Pennington (1991). This family presents a tropical or subtropical amphiatlantic disjunct distribution as it has been observed in other eudicot groups. Sideroxyloae, a clade in this family of about 80 species and probably younger than the 100 My estimated for the family, including the three genera *Argania* Roem. &Schult., *Sideroxylon* L. and *Nesoluma* Baill. This tribe has a wide geographic distribution spanning mainland particularly in Africa, America and the islands of the Indian Ocean and exhibits a great ecological variation, ranging in arid and semi-arid areas as well as in rainforests (Smedmark & Anderberg, 2007). Considering the relatively low number of species, Sideroxyloae has a wide geographic distribution spanning for example Africa (four spp.) and Macaronesia (two spp.). While, *A. spinosa* is the unique representative of Sapotaceae in north western Africa (mainland). The current disjunctive pantropical distribution of Sideroxyloae is due to a relict of a continuous range in the northern hemisphere during a period of warm climate in the early Tertiary (Smedmark *et al.*, 2006). The contemporary distribution of extant species in Sideroxyloae is primarily the result of a rapid radiation in the northern hemisphere in the early Tertiary, followed by extensive extinctions and vicariance process around the Eocene/Oligocene boundary — caused by the barrier posed by the cooling and drying climate— (Smedmark & Anderberg(2007). Then tropical elements were forced toward the equator because of the decreased temperatures (Collinson *et al.*, 1981). In fact, extant species of tropical rainforests are found, e.g., in Macaronesia regions known to have acted as refugia for boreotropical taxa that migrated south in response to the drastic cooling climate in the transition between the Eocene and Oligocene (Morley, 2000).

From the viewpoint of fossil record, pollen from Sapotaceae first appear in the Palaeocene of Europe (Kedves, 1967), and by the early Eocene (*ca.* 50 Mya) the group appears to have become widespread. From the Eocene, pollen types of the main lineages of extant Sapotaceae have been found in most continents (Harley, 1991), and the presence of fossil Sapotaceae pollen both in Europe and in North America indicates that Sapotaceae was part of the boreotropical flora (Morley, 2000).

With reference to the distribution of Sapotaceae in higher latitudes than North-Africa, palynological studies carried out along the Cenozoic in Iberian peninsula indicate the presence of the boreotropical flora, including Sapotaceae pollen but contrary to what might be expected the *Argania* pollen *sensu stricto* is not present, even after the crisis of the Messinian (Barrón *et al.*, 2010 and personal communication). This leads us to think that due *A. spinosa* belong to ancestral pantropical flora lineages which were forced toward equator latitudes around 34 Mya in response to cooling, it expected it has maintained its distribution range in the African subtropical climate zone since pre-Quaternary periods.

Before phylogenetic analyses having (e.g. Smedmark & Anderberg (2007), the information available maintained that the appearance of argan tree dates from the Tertiary era, when it was widespread throughout Morocco (Boukhobza & Pichon, 1988). Quézel & Barbero (1993) hypothesized that argan spread had taken place during the Miocene-Pliocene era. The latter hypothesis was strengthened by the finding of Lower Miocene macroremains in Sardinia (Italy) attributed to *Arganioxylon sardum* (Biondi, 1981), taxon very similar to *A. spinosa*. The evidence above could suggest that the pre-Quaternary origin of the argan tree and its past distribution outside the tropical

zone (Dupin, 1949; Ehrig, 1974; Benabid & Fennane, 1994; Msanda *et al.*, 2005). In fact, according to Emberger (1939), *A. spinosa* despite being a relic of the Tertiary, this species developed under different ecological requirements (e.g. arid climate) from other species included into the genus *Sideroxylon* from which *A. spinosa* was transferred. Cytogenetic studies supported the above hypothesis, showing that the chromosome numbers in the argan tree is $x = 10$, the lowest so far identified in Sapotaceae and it is consistent with its specialized ecology (Majourhat *et al.*, 2007, 2008). Far from admitting assumptions, the oldest and unique evidence of *Argania* pollen *sensu stricto* in North Africa comes from the Western Sahara (Algeria), roughly 300-250 kyr (Beucher, 1967).

The following are the Quaternary pollen sequences taken into account for this study.

The best known fossil record sequences in continental Morocco did not document the *Argania* pollen presence. In fact the pollen data from 8 Holocene peat bogs located in western Rif Mountains, -Daya Arbatète (#1), Bab Taza/Fifi (#2), Marzine (#3), Tanakob (#4), Bou-Hachem (#5) and Jbel Tizirène (#6) (3 cores)- (Reille, 1977; Reille *et al.*, 1996), the El-Khil (#7) and Kaf That El-Ghar (#10) Neolithic caves (Ballouche, 1988; Ballouche & Marinval, 2003), as well as the Palaeolithic rocks helter of Benzú (Ramos *et al.*, 2008) are depressed of *Argania* pollen. The lack of argan pollen has also been detected in Oualidia (#11) and Sidi Bou Rhaba (#12) lagoon ecosystems, located in the central and northern atlantic coastal respectively - both span the last 6500 yr BP-, as well as in the pollen records of Zerga (#8) and Bokka (#9) lowland lakes, which chronology covers the recent Holocene (Reille, 1979; Ballouche & Carruesco, 1986; Ballouche *et al.*, 1986; Ballouche & Damblon, 1988; Peglar *et al.*, 2001). Finally, argan pollen is also absent from a lot of Late Pleistocene and Holocene pollen records (from lakes and peat bogs) from the whole of Atlas Mountains (including the Moulouya Basin): Tessaout (#14), Tizi N'Inouzane (#15), Tigalmamine (#16), Taguelmam n'Harcha (#17), Iguerda-Ait-Amana (#18), Aguersif (#23), Col de Zad (#24), Tirsal (#25), Agdal de l'Oukaimeden (#26), Sidi Ali (#19), Dayat Iffir (#20), Dayat Afourgagh (#21), Aït Blal (#22) and Ifrah (#28) (Reille, 1976; Ballouche & Damblon, 1988; Lamb *et al.*, 1989, 1991, 1995, 1999; Lefèvre & Ballouche, 1991; Lamb & van der Kaars, 1995; Reille *et al.*, 1996; Rhoujjati *et al.*, 2010). From The LGM to the Holocene the pollen record is also lacking from a deep-sea core (Marret & Turon, 1994) (#33) near the coasts of Rabat.

Nevertheless, the argan pollen is present during the recent Holocene in Daya Tighaslant (#13) (Anti-Atlas/High Atlas transition mountains) and Oued Kert (#27) (Eastern Moroccan Rif) sequences, although in both cases with very low percentages (c. 1%) (Bernard & Reille, 1987; Reille *et al.*, 1996; Barathon *et al.*, 2000). Instead, the most important argan pollen percentages (c. 7%) were recorded in the morpho-sedimentary holocene sequence from the Tissouirine snailery (#29) (ancient Neolithic; c. 6000 yr BP), period in which a clear trend towards aridity of the climate is observed. This aridity trend led to a sharp decline of forested area occupied by *A. spinosa*, *Ephedra fragilis* and Fabaceae type *Cytisus*, without obvious symptoms that the deforestation was caused by human impact (Chennaoui *et al.*, 2005). The Tissouirine snailery site is located within the current argan distribution area in the Southwest of Morocco (Fig. 1). Finally, as discuss above, the unique evidence of *Argania* pollen in Western Sahara (Algeria) comes from the Oued Farès (#32) (Ougarta Mountains) during the Ougartian period (c. 300-250 kyr) coinciding with a general climatic shift from a humid to a dry phase (Beucher, 1967).

In spite of this, the major source of *Argania* pollen during the Quaternary were derived from marine sediments (Fig. 1), which increase the uncertainty about its geographical origin, for the reason that they integrate palynological information from large regional areas. Among these evidences are included the results provided by Bout-Roumazielles *et al.* (2007), performed on sediment deposited in the Alborán Sea (ODP 976) (#30). The presence of *Argania* pollen during Heinrich events (HE) took place along the last cold periods — HE1 (~16.8 kyr) and HE4 (~38 kyr) —, indicates Morocco as the main origin for pollen. Additionally, the comparison of the argan pollen with clay mineral-specific features, allow the authors to pinpoint the South-western Morocco (in the vicinity of Western Sahara) as the dominant source of wind-blown particles during North Atlantic cold events.

The second evidence was provided by McGregor *et al.* (2009) in Cape Ghir (#31) (Essaouira, Southern Morocco). In a tentative for interpreting the origin of the argan pollen found in the marine sediments, the authors indicate Southwest Morocco as the possible sources. The pollen data shown that the argan woodland has been growing in the Southern Morocco region for at least the past 2000 years, with an increased by 1000 yr AD. Consequently, these data confirm that there is an overlap between the current argan woodland range and the occupied 2000 years ago. In any case the bit extensive chronology of the sequence do not permits emitting hypothesis about the Quaternary argan woodland extension.

Climate scenarios for Morocco

Figs. S1 and S2 show respectively the summarized values from the Moroccan climate projection (past climate: CCSM and MIROC; and 2080 future climate: HADCM3; CSIRO; CCCMA) with respect the current climate data. At the LGM a cooling of 2,6 °C and 0,7°C (Tann) (MIROC and CCSM simulation, respectively) was detected. Contrary to expectations, driest conditions were not found during the LGM. Rainfall was more abundant than at present, with anomalies of up to 464 mm and 466 mm (MIROC and CCSM simulation, respectively). Opposite to LGM, at the Middle Holocene no significant anomalies for Tann (a reduced amount of 0.21°C) and Pann (266 mm fewer) were observed, note that as lightly drier scenario was found at this period. The SRES scenarios of A2a and B2a for 2080 show an important increased from modern values, estimated at average around of 2,76°C for Tann. In addition a significant difference was detected with the precipitation values for 2080 (88mmlessthancurrent annual values).

Model accuracy and prediction uncertainty

Despite our modelling approach relies on a combination of robust methods, and the resulting SDMs for *A. spinosa* are among the best that can be achieved for our dataset (presence and environmental data), there are several possible sources of error which must be taken into account before interpreting results.

Unfortunately, the lacks of fossil data to validate the projected past distribution for LGM do not permit quantitatively assess the proportion of fossil occurrences of pollen within the projected climatic niche for *A. spinosa*. Futurity, the finding of any more pollen deposit (wetlands or lakes) inside the suitable area projected by the algorithms could allow us to validate the model prediction ability.

Additionally, calibrating the species' climatic niche under current conditions and projecting them to non-analogues conditions into the past could lead to spurious

response curves and therefore would design simple projections (Thuiller *et al.*, 2004; Pearson *et al.*, 2006). Furthermore, there are many possible sources of error and uncertainties involved SDMs projections through time, including a number of strong assumptions, such as equilibrium of species distribution with climate, stability of climatic niches through time, etc. (see Nogués-Bravo, 2009).

An added complication may arise because the PMIP model data underestimated the drying and cooling throughout the Mediterranean Basin at the LGM (Ramstein *et al.*, 2007) and so the models presented could overestimate the *A. spinosa* distribution during the Last Glacial Maximum. In addition, according to the authors cited above, the spatial resolution of the PMIP models may be a supplementary difficulty, particularly in areas of complex topography such as Atlas Mountains. Enhancing the models' resolution should improve the representation of a given region, but it remains unclear whether the sensitivity of the models will be affected by changing their resolution. In parallel, and according to Boberg & Christensen (2012) it is likely that many climate models overestimate regional amplification of global warming. This overestimation could also be inducing to grave errors in the projection of the species under future climate scenarios in the Mediterranean.

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FIGURES

Figure S1 {Additional information concerning annual temperature (T_{ann}) in the different climate scenarios is shown. The diagram display the T_{ann} variation during four periods —LGM, Middle Holocene, present-day and 2080— the past periods under two general circulation model estimates (CCSM and MIROC) and future period under HADCM3, CSIRO, and CCCMA. Boxplot (the bottom and top of the box are the lower and upper quartiles, respectively; and the band near the middle of the box is the median) with whiskers from minimum to maximum values}

Figure S2 {Additional information concerning annual precipitation (P_{ann}) in the different climate scenarios is shown. The diagram display the P_{ann} variation during four periods —LGM, Middle Holocene, present-day and 2080— the past periods under two general circulation model estimates (CCSM and MIROC) and future period under HADCM3, CSIRO, and CCCMA. Boxplot (the bottom and top of the box are the lower and upper quartiles, respectively; and the band near the middle of the box is the median) with whiskers from minimum to maximum values}

Figure S3 {Additional information concerning potential distribution of *Argania spinosa* in present and paleoclimate scenarios when the two isolated population (red circles) were removed from the presence dataset in the model building processes —LGM (exposed shelf areas are shown) and Middle Holocene under two general circulation model estimates (CCSM and MIROC)}

Figure S4 {Additional information concerning argan potential area (ha) estimated by SDMs (GLM, Maxent, Mahalanobis and Boosted Regression Trees) in the different climate scenarios. The diagram displays the variation during six periods –LGM, Mid-Holocene, Present, 2020, 2050 and 2080. Past periods are the mean value for the two general circulation models (CCSM and MIROC), future periods are the mean value for three general circulation models (HADCM3, CSIRO and CCCMA)}

Figure S5 {Additional information concerning the predicted potential distribution areas for *Argania spinosa* in future periods (2020 and 2050)}