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Multidisciplinary approaches for conservation issues

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"The essence of Darwinism lies in a single phrase: natural selection is the creative force of evolutionary change. No one denies that natural selection will play a negative role in eliminating the unfit. Darwinian theories require that it create the fit as well."

— *Stephen Jay Gould*

Introduction

In the current global warming context, mountain tree species need to adapt locally within their modern range (Sexton et al. 2009; Aitken et al. 2008; Hoffmann & Sgro 2011) or migrate (Malcolm et al. 2006; Williams et al. 2007) to more climatically suitable areas. If these two options cannot be accomplished then at best the species will persist in a restricted range as small population(s) (Araújo & Williams 2000; Keppel et al. 2015) under a suitable local (micro)climate or might turn extinct. Mountain species in Europe are considered highly sensitive to climate change with 60% of them threatened with complete extinction by 2080 (Thuiller et al. 2005; Thomas et al. 2004). The involved mechanisms seem complex. Steinbauer et al. (2018) demonstrated that mountain summits became enriched in species at an accelerating pace during the last decade and that the new colonizers show traits which are typical of lower altitudes species. They suggested that this phenomenon will later result in the impoverishment of the initial diversity by competitive replacement. At the global scale, observed changes indicate a sustained decline in cold mountain plant communities in response to the recent warming while the climatic impact seems more pronounced in areas with a marked increase in temperature (Gottfried et al. 2012). The International Union for Conservation of Nature (IUCN) reported about 800 extinctions in species over the last 500 years, with more extinctions that have probably not been inventoried. Species extinction is a natural process that one may observe in the geological records (Darwin 1872). However, in the natural process a species may persist for few millions of years (Raup & Sepkoski 1984).

Fossil records contain information on how plant species have responded to past climate changes over the geological periods. Spatial data syntheses allow us to depict where species have persisted during past periods when climates were not suitable (Bennett & Provan 2008) and how they expanded their range to more suitable habitats (Jackson & Overpeck 2000) when climates became more favorable. Fossil records also allow us to depict periods of times when species became extinct (Magri et al. 2017). Expected rapid climate changes during the next century will likely induce noticeable changes in the species ranges and will impact their potential extinction rates (Thomas et al. 2004; Thuiller et al. 2005). The modern challenge is that the velocity of the ongoing global climate change exceeds the known migration rates of the many plant species composing major global ecosystems (Loarie et al. 2009; Dobrowski et al. 2013, Corlett

& Westcott 2013).

The expansion/regression and adaptation/extinction processes which have taken thousands of years may occur within the next century. This is why scientists are exploring different options to preserve those species which may not be able to neither migrate to more suitable habitats nor adapt locally in such short period of time (Aitken et al. 2008).

The objective of this chapter is to show that the integration of different but complementary disciplines such as palaeoecology, genetics and species modelling can provide us with pertinent information on the environmental changes which have impacted plant species across time and therefore, can contribute to setting better strategy for preserving species. Genetics allow us, for instance, to evaluate the infra-specific diversity between and among populations (Petit et al. 1998) and the overall capacity of a species to cope with strong environmental changes (or not). Meanwhile, vegetation model simulations may provide useful information on the geographical range changes through time and help predict future suitable areas for the species persistence (Pearman et al. 2007; Maiorano et al. 2013). Palaeoecological data allows us to evaluate the past relationships between plant species and their contemporaneous climate which can contribute to a better management of the future plant/environment relationship (Gillson & Marchant 2014; Petit et al. 2008; Willis et al. 2007). These disciplines are of particular interest to the conservation of mountain tree species which often represent a great value to the ecosystem services they provide (Schröter et al. 2005). The mountain landscapes of Morocco have been declared by UNESCO as a critical habitat for conservation, justifying the recent inclusion of the Atlas Cedar Biosphere Reserve (Sarmiento 2011).

A multidisciplinary approach for a better species conservation?

One of the goals of conservation is to prevent species from becoming extinct. Thus, one of the key conservation aims is to identify the threatened species, evaluate the degree of the threat, identify putative regions where the species may be preserved, and consider the environmental conditions that are suitable for the survival of the species. Thus, a scientific-based management strategy for preserving species requires the integration of several disciplines such as ecology, climatology, genetics, and modeling. In order to be pertinent and efficient at managing species under any different climate from that of today, we need this integrated multidisciplinary approach within a historic data frame.

Palaeoecology is the study of the interactions between species and their environment, including climate, over geological timescales. The study of these interactions provides a scientific basis for evaluating a species capacity to cope with climate fluctuations, its capacity for migration or the suitable areas for its potential occurrence. Thus, palaeoecology can provide sound interpretations that can be directly used for species conservation. Fossil pollen grains are one of the most used biological proxies in vegetation palaeoecology for reconstructing past plant-environment relationships. Their excellent preservation in sediments is due to sporopollenin, one of the most resistant biological substance to degradation, which constitutes their ornamented and recognizable outer wall. The highest number of fossil pollen records available cover the last 20,000 years which is a period of time that covers the last glacial maximum and its transition to the Holocene warm period where the human population massively colonized the planet. Fossil pollen records contain information on the occurrences of all the local species through time. A data set of well-dated fossil records allows for the spatial reconstruction of past species occurrences at different time periods

and spatial scales (Brewer et al. 2002). Using these spatial past occurrences across time, one can evaluate the evolution of the species range over time and the velocity of the spread (Cheddadi et al. 2014; Huntley 1991). These estimates may provide us with information on whether a species may cope with a climate warming scenario or not.

Fossil pollen data sets can also provide essential information on the past ecosystems composition and dynamics (Overpeck et al. 1990), the species richness through time (Svenning & Skov 2007), the competition between species (Clark & McLachlan 2003), the abundances of the species composing the succession of ecosystems through time (Bennett 2004), the prevalence of a species over the others, the expansion and extinction of species (Jackson & Weng 1999) when climate changes and so on. All these past ecological parameters are essential for vegetation modelers and conservation managers. Quantifying ecological variables can be directly applicable to conservation managers to (1) identify whether there is a risk of extinction, (2) develop realistic plans for conservation in suitable areas, and (3) to identify appropriate management tools for maintaining or, if at all possible, restore the *ad hoc* ecological settings. Basing conservation decisions on a long-term ecological perspective will undoubtedly be of a more robust approach than only on contemporary observations (Willis et al. 2007) and the inclusion of a long-term ecological perspective can provide a more scientifically defensible basis for conservation decisions than the one based only on contemporary records.

Vegetation models are required to predict future species distributions and potential suitable areas and habitats for their conservation (Pearman et al. 2007; Sykes et al. 1996; Prentice et al. 1992). However, reconstructing past ecological parameters of a species from fossil data sets is essential for validating and improving the vegetation models (Maiorano et al. 2013; Cheddadi et al. 2016). There are basically two types of models describing the geographical distribution of plant species: the ecological niche-based models (ENMs) and the process-based dynamic vegetation models (DVMs). ENMs are empirical relationships between plant species occurrences, or more rarely abundances, and spatial climate datasets (e.g. Guisan & Thuiller 2005). ENMs don't take into account the atmospheric CO₂ concentration which has a direct impact on the plant tolerance to water stress. DVMs are more complex tools that combine, in a chronological process schemes and feedbacks, both inputs and outputs of sub-models. Beside species distributions, DVMs compute productivity and other ecological variables (e.g. Dury et al. 2011; Snell et al. 2014). The sub-models are designed to compute environmental conditions at plant level (e.g. water availability, CO₂ concentration inside the leaves, photon flux etc.) from environmental data (including climate) and physiological processes describing plant functions and allowing growth and development (e.g. stomatal aperture, fixed carbon allocation. So far, DVMs are rather limited by the lack of specific information required for each species to be simulated (i.e. plant traits).

More recently, environmental DNA (eDNA), a powerful past environmental proxy, has been developed and is experiencing an unprecedented boom for reconstructing past plant occurrences from the fossil records (Taberlet et al. 2012; Willerslev et al. 2014). eDNA already allows us to identify much more organisms (plant and animals) in a fossil record, that have lived in the past ecosystem (Giguet-Covex et al. 2014; Pansu et al. 2015) which represents an essential information for conservation managers on the habitat suitability and the co-existence of plants/animals species within a specific environment. The ongoing development of eDNA is expected to provide even more accurate and efficient information on past plants occurrences and their direct environment.

Conservation of the Atlas cedars in Morocco

State of the art

Cedrus atlantica (Atlas cedar) is a North African mountain conifer tree that may withstand strong droughts (Aussenac & Finkelstein 1983; Aussenac & Valette 1982) that are higher than any European temperate coeval mountain tree species. However, the aridification trend recorded over the last century has already impacted its range with a migration of its lower viable elevation limit by about 200m in the Middle Atlas (Rhanem 2011) and a substantial reduction of its range in the Rif Mountains (Cheddadi et al. 2017). The increase in winter temperatures (Ezzahiri & Belghazi 2000) and the recent successive years of soil droughts (Ladjal et al. 2005) seem to affect its growth as well. Tree-ring data has allowed us to observe the negative impact of the recent recurrent droughts and temperature increase on its growth (Linares 2011). The Atlas cedar is now considered an endangered species by the IUCN (<http://www.iucnredlist.org>). Forest managers in Morocco are now protecting some populations with fences and replanting seedlings around existing populations which show a strong trend in population decline. Indeed, locally, grazing, poaching, and inadequate management still hinder regeneration (Navarro-Cerrillo et al. 2013) while replanting is not 100% successful.

What is the approach?

In order to evaluate the impact of past environmental changes on the Moroccan Atlas cedar and contribute to its conservation we need to identify the areas of concern with potentially threatened populations and propose a strategy based on both the scientific facts and a realistic strategy for conserving the species over the long term. Our approach is based on reconstructing past climates and species occurrences from fossil records, simulating its past ranges using a vegetation model and evaluating the species genetic diversity through an exhaustive genetic survey of the modern populations. The target area is located in the northernmost part of the Atlas cedar distribution in Morocco. We collected several geological corings from the Rif mountains at different altitudes and distances from the modern Atlas cedar forests. Then we sampled the modern populations for their DNA study before finally using a DVM to simulate the evolution of the Atlas cedar productivity and range in the Rif mountains continuously over 50 years between 1960 and 2010.

What does the data say?

We know from fossil pollen records that *Cedrus* sp. was present in the Mediterranean borderlands since at least 2.6 Ma (Magri et al. 2017) including Northern Morocco during the Pleistocene (Feddi et al. 2011). How did the species persist throughout several climatic cycles with marked alternating glacial and interglacial climates?

The fossil record

Fossil records allow us to track species occurrences in space and time. However, there are several physical limitations in arid areas, such as North Africa, to the accumulation of sediments and the preservation of fossil biological environmental proxies in continuous records encompassing more than the last glacial period and the Holocene. As a matter of fact, there are very few records encompassing more than the last 20,000 years. These available geological records contain vegetation and climate proxies that help us reconstruct past species occurrences and past climate variability. The fossil proxies help reconstruct and then interpret the relationship between species and their contemporaneous climate over the time period covered by the record.

The pollen records available in the Rif Mountains indicate that Atlas cedar populations were present at much lower altitudes than today, near the Mediterranean Sea (Linstädter et al. 2016; Zapata et al. 2013). Today, Atlas cedar occurs at altitudes higher than 1400m above sea level (asl) in a more reduced and fragmented range than during the last glacial period at lower elevations (figure 1). Based on several fossil records from the Rif Mountains, we can observe that the Atlas cedar had a much more extended range around 6000 BP with extensive populations down to 800 masl or probably at lower elevations. The 600 meter migration upwards to the modern 1400 masl took place over the past thousand years after 6000 BP. These expansion/regression spatial movements during the Holocene allow us to evaluate the response velocity of the Atlas cedar to the climate forcing that may be inferred from the climate proxies.

The climate reconstructions (figure 2) that we have performed from the pollen records show that winter temperatures were lower between 7500 and 5700 BP than today. This time span was also the wettest within the Holocene time period with a more marked increase of precipitation during spring than in the winter season. This cool and wet time interval corresponds to the most extended geographical range of Atlas cedar in the Rif Mountains (figure 2). These past climate data tend to suggest that even if the Atlas cedar is rather well-adapted to drier climates than many other conifer species, it may show a more sustained growth and expansion of its range under a wetter and colder climate than today. These past climate interpretations are coherent with the genetic data and confirm that the species expanded its range during the last glacial period, more probably at lower altitudes towards the Mediterranean Sea (Linstädter et al. 2016; Zapata et al. 2013) where some moisture may be available even during cold periods.

The modern genetic evidence

The modern genetic data reveal very low divergence between populations and do not support a recolonization process from isolated population(s) (figure 3) but rather a persistence of at least one large population which has fragmented in the Moroccan mountains by extinction at lower elevations. This process prevented from a marked genetic drift and lead to the modern low genetic differentiation in the whole range of the species and maintained the occurrence of all haplotypes in all populations. Indeed, previous genetic surveys carried out on the modern populations of Atlas cedar in Morocco show that there is no clear geographical diversity structure (Terrab et al. 2006; Cheddadi et al. 2009) which tends to suggest that since pollen does not disperse far from its originating Atlas cedar tree (Wright 1952; Hajar et al. 2008), the most likely explanation is that Moroccan populations are the result of a massive colonization event, without founder effect. According to the ecological requirements of the species, such colonization happened during cold periods when the potential distribution area was probably continuous.

The model simulations

DVMs may help identifying potential suitable areas and evaluating the risk of extinction of a species under different climate scenarios. To assess the impact of the past climate changes on cedar populations, we run a model simulation continuously over the past 50 years, between 1960 and 2010 (figure 4). Our model simulation (Cheddadi et al. 2017) provided three major information: (1) that the range of Atlas cedar in northern Morocco decreased by about 75%, (2) that those populations located at the easternmost part of the range are heavily threatened by the decrease of the water availability, and (3)

that populations at lower elevation are strongly impacted which lead over the past few decades to an upward lift of the lower limit of the distribution by about 200 meters. The latter is coherent with observed data in the Middle Atlas (Rhanem 2011).

What do we do with this scientific data?

Today, Atlas cedar populations in Northern Morocco occur in quite restricted and fragmented areas. The main populations are located in Jbel Kelti, Talassemtane National Park, Jbel Tiziren, Targuist, Oursane and Tidighine and they occupy less than 12k ha. The populations in Jbel Bouhachem have strongly declined with many that turned extinct over the past few decades. There remains only one very reduced population that is almost close to extinction. Our model simulations show that the occupied range was about four times higher (40k ha) in 1960-70 than today which is coherent with the IUCN status of *Cedrus atlantica* which states that the species is "endangered with a decreasing population trend" (<http://www.iucnredlist.org>). The fossil data have recorded an even more extensive range 6000 years ago and the genetic survey confirm the presence of few and very extended populations in Morocco since there is very weak genetic structure between the isolated modern population.

Thus, based on our multidisciplinary and multi-scale approach, we consider the modern populations of Atlas cedar in the Rif Mountains as relic populations that are persisting today in microrefugial areas which offer a habitat that has a suitable microclimate. However, these populations are quite distant from each other which prevents the gene flow between them. Such genetic isolation may lead to a collapse of all these remnant populations on a more or less short term.

To maximize the chances of persistence for the Atlas cedar in its endemic range we may propose (1) as a basic rule, to protect all the remaining microrefugial areas from any human disturbance, mostly seedlings at the upper limit of each population since the species requires cool and wet conditions which may be still available at higher elevations; (2) to evaluate quantitatively the microclimate suitability in each microrefugial area with a dedicated system for climate monitoring; (3) eventually, to transplant seedlings into new areas that are unoccupied today by the Atlas cedar but which have been identified by the model simulations as potentially suitable new microrefugial areas under different climate scenarios; and (4) since the modern populations are too remote to have any gene exchanges, we could also consider some gene exchanges between them which could improve heterozygosity and potentially the capacity of the successful hybridized generation to adapt locally.

Conclusions

The aim of this work is to highlight the importance of combining information from different but complementary disciplines within a multi-scale approach for building a reasonable scientific basis that may contribute to species conservation. This approach is being developed within the VULPES project (www.vulpesproject.com) for other species in South America, Tropical Africa and China.

The case study chosen here is the threatened species *Cedrus atlantica* in Northern Africa which persists as few remaining and geographically isolated populations.

The combined data that we have collected and analyzed tend to indicate that the areas where the Atlas cedar populations are persisting today should be considered as microrefugia with a microclimate that is still cooler and wetter than the average climate in Northern Morocco where snow still occurs, although not every year, during winter (figure 5).

The future persistence of the remaining Atlas cedar populations in the Rif Mountains will depend on the long term natural climate stability of these microrefugia and the management strategies. Generally, one may observe that the human impact is not as strong in the Rif mountains as in the Middle Atlas because the remaining populations are not so easily accessible such as in Jbel Kelti, Talassemtane National Park or Jbel Tiziren.

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