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## Chapter n°13

# Climate change impact on vegetation: lessons from an exceptionally hot and dry decade in south-eastern France

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### Abstract

The ongoing climate change causes a rapid shift of plant distribution at various scales. In South-eastern France from 1998 to 2008, Mediterranean forests experienced an exceptionally hot and dry episode following a regular but more limited warming since the 70's. Flora turnover for this period was both simulated at local scale with a bioclimatic model and measured in permanent plots with two censuses. Model prediction for this turnover with the mean climate of the last 10 years was 25%. A 14% turnover was observed in the permanent plots between the two censuses, fully biased against water demanding species. Changes were all the more fast than sites were favorable (high altitude, cool orientation, deep soils, favorable topography), and were not significant in the driest and hottest sites. This suggests that the main changes occurred when the compensation of climatic water deficits by local site favorable conditions was no longer sufficient to allow mesophilous species to survive. Such a threshold should shift towards hottest and driest situations with the future climate. On the landscape scale, various strategies allow a partial plant composition resistance. However, current reserve networks may be inadequate to ensure long-term species persistence. With the measured flora shift, most of the rare species protected in these reserves would potentially disappear from the study area soon in the second half of the 21<sup>st</sup> century.

### Keywords:

*Climate change; flora turnover; resurvey; bioclimatic model; ecological niche; reserves*

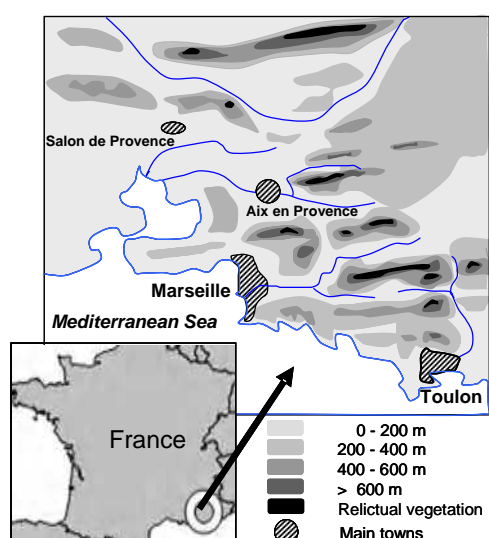
## 1. Introduction

For the 21<sup>st</sup> century, all climatic models predict in the Mediterranean basin a faster warming than in most other continental areas of the world, associated with a reduction of rainfall during the growth season (Hesselbjerg-Christiansen & Hewitson, 2007). As warming is likely to be larger in summer, extreme climatic events such the 2003 scorching heat (Ciais et al. 2005; Zaitchik et al. 2006) are prone to be recurrent. Drought being already the main limiting factor for Mediterranean vegetation (Le Houerou, 2005), many species should be at risk with repeated critical water stress during the growth season (Breda et al., 2006).

According to several studies, (Hughes, 2000; Lenoir et al., 2008) the track race between climate change and vegetation is already launched. Many species looking for suitable habitats move towards the poles or upwards in elevation (Walther et al., 2005). However, mean plant dissemination distance is short (Clark et al., 1999). Certain plants may be unable to follow the edges of their potential distribution area, as fast species spread recorded at the end of ice ages (Delacourt & Delacourt, 1987) are slower than the expected limit shift in the 21<sup>st</sup> century (Thuiller, 2004). Species shift should be checked by biotic interactions (Preston et al., 2008) and competition. Time lags in plant phenology (Menzel & Fabian, 1999) could make them more vulnerable to meteorological extreme events (Morin et al., 2007). Altered architectural development and sexual reproduction (Hedhly et al., 2009; Thabeet et al., 2009; Girard et al., 2010), may also hamper their growth and dissemination. Mediterranean small mountains offer to Alpine or middle-European vegetation fragmented but suitable relict niches mainly near their top (*figure 1*). Inherited from former climate conditions, mixing several biomes in small areas, these niches are biologically very rich (Médail & Quézel, 1999) with a high level of endemism. But future climate warming raises their potential

trailing edge over local summits (Trivedi et al., 2008b). In the absence of functional corridors, current reserve networks may be inadequate to ensure the long-term persistence of these species (Araujo et al., 2004). However, on local scale, site conditions including deep soils and steep northern slopes at the highest elevations may create refuges. Such a precise assessment of favourable sites is not easy with existing models. Although many types of models were used to assess the evolution in plant composition with climate change, computing potential distributions, bioclimatic limits or niches (Botkin et al., 2007; Hansen et al., 2001), for individual species (Gaucherel et al., 2008; Heikkinen et al., 2006) or species groups, very few of them tackled local scales (Trivedi et al., 2008b). This is why we recently developed a new bioclimatic model, based on a flora census, taking into account both local and global variables (Table 1) (Vennetier et al., 2008) in order to bridge regional to local scales. One of the possible uses of this model is to assess the potential flora composition turnover with different simulated climate scenarios (Vennetier et al., 2009).

Flora composition is often considered as a good indicator of site conditions, including site and climate parameters (Berges et al., 2006). A hotter and drier climate should lead to a significant flora turnover biased towards heat and drought tolerant plants. However, if the speed of an altitudinal or latitudinal species shift



was often assessed in literature, the turnover was rarely documented on local scale. During the decade 1998-2008, south-eastern France experienced an anticipated occurrence of what should be the climate around 2040 according to IPCC B2 or A1B scenarios (Christensen & Christensen, 2007). It was interesting to assess whether these exceptional conditions were reflected in flora composition.

The aims of this study were (i) to measure plant composition evolution in a permanent plot network between 1998 and 2008, (ii) to compare the observed evolution with the potential turnover computed with our model (iii) to disentangle the relationships between observed changes and local site conditions.

Figure 1: study area. Alpine and middle-European relict flora remains on steep north slopes near the top of the highest ridges.

## 2. Material and method

### 2.1. Study area and sampling

The study area is situated in the French Mediterranean area (figure 1; long 4°5' - 6°2' E, lat 43°4', 43°5' N). The climate is characterized by a long summer drought (2-4 months) and mild rainy winters. The mean annual temperature and rainfall range respectively from 15.3°C / 500 mm on the Southwestern coast to 9.5°C / 1000 mm on the highest ridges (around 1100 m), with an average of 13.2°C / 720 mm. *Pinus halepensis* Mill. and *Quercus ilex* L. are the main forest tree species along the coast, at low elevation and on shallow soils, while *Quercus pubescens* Will. is all the more abundant as elevation, continentality and soil depth increase.

The sampling plan was design to be representative of the span of local and global site conditions, crossing the main ecological gradients: soil quality, topography, orientation, climate, continentality (Table 1). In order to minimize the role of disturbances in vegetation response, we selected only sites with no registered disturbing activity such as logging, grazing, clearing, or prescribed fire over at least the last 30 years. In most of these sites, dominant trees were more than 70 years old. Initially, 325 forest plots (400m<sup>2</sup> each) were surveyed between 1996 and 1998. A thorough description and measure of site conditions was performed, along with a flora census using Braun-Blanquet abundance-dominance scale (Braun-blanquet 1932). The flora census was done again in 2008 on a representative sub-sample of 50 plots.

## 2.2. Model bases

The main output of the model, previously presented by Vennetier et al. (2008), is a bioclimatic index. This index combines two components: the first one is based on variables which can be mapped by GIS from local to regional scale (climate, continentality and orientation); the second one is based on variables which can be precisely observed only on site scale (soil, local topography). In this section, only the bases of the model which are useful for this study are explained. Statistical procedures are described in *annex 1*.

The model was designed in two steps.

The first step was a correspondence analysis (CA) on plant composition with the 325 plots, keeping 192 species present in at least 3 plots. *Figure 2a* shows a synthesis of the main CA plane. When displayed as supplementary variables in this plane, all variables relevant in terms of water balance or temperature, and which could be grouped in four main gradients, were linked to axis 1. All their classes related to unfavourable conditions (low water availability, high temperatures) were found in the left half of the plane and favourable classes in the right half. Considering its dominance (eigenvalue twice the one of second axis), this first axis was retained alone for modelling and considered as a synthetic bioclimatic gradient.

When displayed in the same plane, plant species are sorted along axis 1 in the synthetic gradient. According to their coordinate on this axis, they can be split into five groups of equal number from the left (the most heat and drought tolerant) to the right (water demanding ones) (*figure 2.b*): super xero-thermophilous (sXT), xero-thermophilous (XT), intermediate (Int), slightly mesophilous (Meso) and mesophilous (Meso+). Plots can be displayed in the main CA map. As their position is only determined by their flora composition (plots are at the barycenter of their plants), we considered their coordinate on axis 1 as a Flora index (Fi), sorting them too along the bioclimatic gradient.

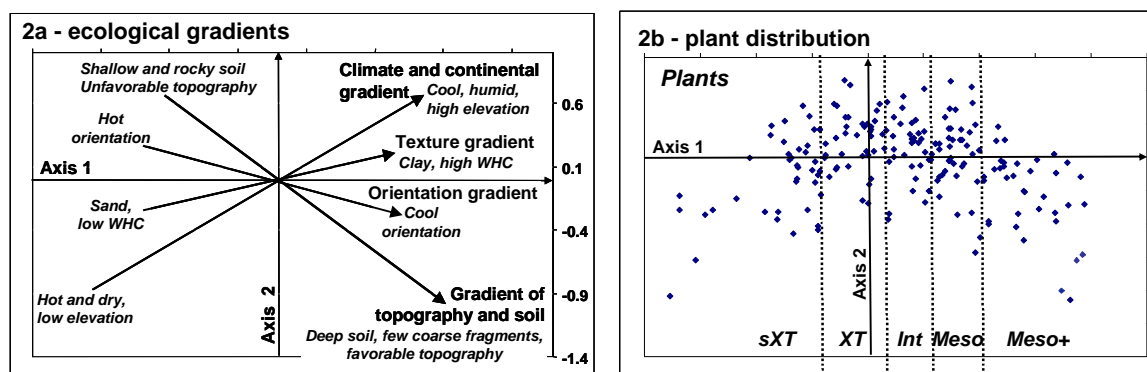


Figure 2: CA main plane

\* fig 2a: synthetic representation of four main ecological gradients related to water balance in the study area, interpreted from the distribution of all variables (see table 1) in CA plane: (1) climate and continentality, (2) orientation, (3) soil texture (water holding capacity), (4) topography and soil quality. These gradients were calculated with a linear regression on the coordinates of the classes of concerned variables in the plane. Axis 1 appeared as the synthesis of these 4 gradients, related to water availability and temperature, integrating local and global scales.

\* fig 2b: flora distribution in CA plane. Plant species were split into 5 groups (same number of species in each) according to their coordinate on axis 1.

The second step consisted in computing a bioclimatic index (Bi) for each plot. Bi is the estimate of Fi with a Partial Least Square regression model using abiotic explanatory variables describing site conditions. *Table 1* presents the height global and six local relevant variables. The model explained 81% of Fi variance. Thanks to the good fit between Fi and Bi, and to the key role played by climate variables in the model, the impact of climate change on plant composition can be assessed as described in paragraph 2.3 below.

**Table 1: variables describing site conditions and used for the model**

	Coef *	Variable description	Gradient in fig 2a
Global variables	-0.183	Becker light-climate index (relative received solar energy in % of an horizontal reference plane)	2
	-0.153	Mean annual temperature	1
	0.131	Altitude	1
	0.115	Summer rainfall (cumulated from June to August)	1
	0.082	Annual rainfall excluding summer, or spring rainfall	1
	0.169	Maximum altitude between a site and the coastline in two directions: the closest coast line and 247°	1
	0.146	Distance to the sea	1
	0.106	Distance to the sea	1
Local variables	-0.136	General topography on landscape and slope scale (5 classes scale)	4
	-0.107	Topography on local scale (plot size) (5 classes scale)	4
	-0.083	Percentage of parent rock outcrops on the plot	4
	0.100	Water holding capacity of earth (mm/cm) based on soil texture	3
	-0.091	Percentage of coarse fragments in the soil	4
	0.119	Total soil depth	4

\* Coef. = Partial regression coefficient in the PLS regression model. All these coefficients are highly significant ( $P < 0.001$ ). They sort variable by their relative weight in the model.

The initial CA, using the flora census of 1996-98, was computed with the climate of the period 1961-1996.

### 2.3. Simulation of climate change impact on plant turnover

The simulation used the two steps of the model:

First, we considered that an increasing mean annual temperature or decreasing spring or summer rainfall would favour xero-thermophilous species, and stress mesophilous ones. We simulated this impact (Figure 3), changing at plant distribution margins of each plot the composition (3b) or the abundance-dominance (3c).

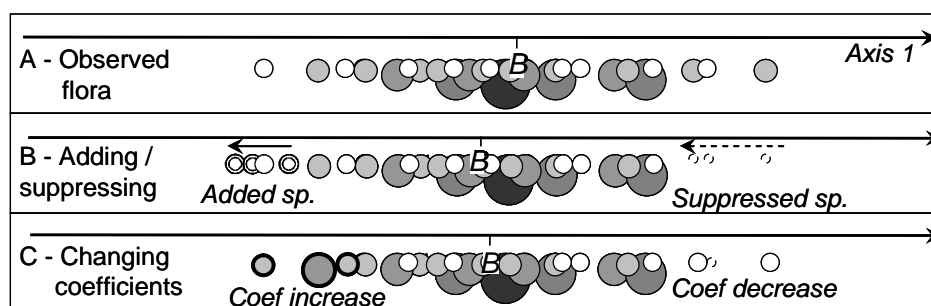


Figure 3: Simulated flora variations with climate change. Each ring represents one plant species, all the more large and dark as its Braun-Blanquet coefficient is high. B = barycentre of plant distribution on axis one for the plot = plot Fi.

3a - Observed flora.

3b - One to 3 plants are respectively added / suppressed at the lower / upper margin of the distribution. Added plants are those with the closest coordinates to the last observed species.

3c - Braun-blanquet coefficients are respectively raised / reduced for one to 3 plants at the lower / upper margin of the distribution. When a plant initially has the smaller coefficient, reducing it amounts to suppressing this plant.

Using these modified plots as supplementary observations in the initial CA, we computed the new coordinates of each plot on axis 1 (Figure 3), which means new and smaller Fi indices (modified plots shifted to the left in the CA plane).

In the second step, we simulated various climate change scenarios, with lessening summer or spring rainfall (-10 to -30%) and raising temperatures (1 to 2°C). We also used in the model the mean climate observed

over respectively the last 10, 20 and 30 years (1978-2007). New and smaller Bi indices for each plot were computed.

The good correlation between Fi and Bi indices enabled linking their respective shift with the flora and climate change simulations, and therefore assessing the plant composition turnover expected for each climate scenario. We did not consider the future of individual or specific plants, but the global turnover as a percentage of plant composition.

#### 2.4. Validation with the new flora census

This census was performed in spring 2008 by the same team using exactly the same protocols. We analysed the flora turnover as the changes in plant presence and abundance-dominance, on one hand with all plants separately, and on the second hand considering the five groups of grading heat and drought tolerance designed in figure 2a.

### 3. Results

#### 3.1. Number of plants per plot

The average number of plants was 25 (7-53, SD= 8) in the 325 initial plots, and 27 (15-48, SD=7.5) in the 50 plots surveyed twice. This average number was unchanged in the last 10 years although its mean absolute variation was 18% (4 - 5 plants), gains in some plots compensating losses in others. The number of plants per plot increased regularly with plot If ( $r^2 = 0.22$ ,  $p < 0.05$ ) ranging from 22 for If lowest fourth to 32 for If highest fourth: as a whole, mesophilous sites were richer than drier sites. However, percentage variations in the number of plants per plot did not depend on If.

#### 3.2. Simulation of climate and plant composition changes

Table 2 sorts the If shift for different simulations of climate change and plant composition change. This relation is given as an average for all plots. For a given number of plants changing at the edge of the distribution margins, the richer the plot and the smaller its span, the less sensible it is to these changes. For example, the change of +2 and -2 plants gave an average shift of 0.181 (SD = 0.063) with maximum / minimum values of respectively 0.503 for a plot with 10 species and a wide distribution and 0.088 for a plot with 50 species and a narrow distribution. As the number of plants affected by climate change may be proportional to their total number, we used percentages of flora composition to express changes, making the results independent of plot specific flora.

Table 2: Fitting flora turnover and climate change impacts with the shift of plot If. The last example of climate change corresponds to the mean climate of the last 10 years (1998-2008) compared to the reference 1961-96.

\* Temperature increase is for mean annual temperature. SumR = Summer rainfall, SpR = spring rainfall.

Simulations		% of flora composition	If shift on axis 1 (mean all plots)
<b>Climate change</b>	<b>Flora change</b>		
-10% SpR or SumR			-0.030
	(1) -1 or +1 plant	4%	-0.050
-20% SpR or SumR			-0.052
+1°C *			-0.074
+1°C -10% SpR or SumR			-0.105
	(2) -1 and + 1 plants	8%	-0.106
	<i>Abond-Domin + 1 or -1 for 4 plants</i>		-0.111
+2°C *			-0.143
	<i>Abond-Domin +1 or -1 for 6 plants</i>		-0.154
	(4) -2 and + 2 plants	16%	-0.181
+2°C -10%SpR and -10%SumR			-0.192
+2°C -20%Spr or SumR			-0.193
+1.4°C -18% SpR and -32% SumR			-0.264
	(6) -3 and + 3 plants	24%	-0.269

A reduction of 20% of spring or summer rainfall corresponded to a change of 4 to 5% in flora composition. Each added °C increased by 7 to 8% flora turnover. The mean climate of the last 10 years led to a potential change of one fourth of plant composition.

For a given plot, the mean shift of If observed with the decrease / increase of one point for the Braun-Blanquet coefficient of a plant was 60% of the shift obtained with the suppression of this plant or the addition of the closer plant.

### 3.3. Comparison with the observed shift in plant composition

The observed shift did not occur at random but was biased towards axis 1 bioclimatic gradient. Figure 4 shows the spatial evolution of flora sorted by plant groups.

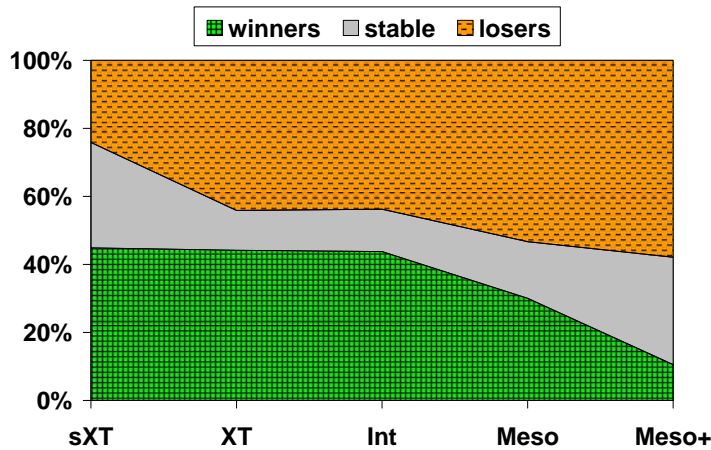


Figure 4: Variation, between 1996-98 and 2008, of the occurrence of plants according to their tolerance to water stress and heat, as a percentage of the number of plants per group. Winners / losers means plant species respectively present in more / less plots in 2008 than in 1996-98.

In the sXT group, nearly half of the plants were winners, two times more than losers. Conversely in the Meso+ and Meso groups, half of the plants were losers, respectively five times and two times more than winners. In the intermediate and XT groups, the turnover was balanced, losers and winners being as numerous, which means that disappearing species were replaced by plants of the same group. 30% percent of the plants remained spatially stable in the two extreme groups, but only 10 to 15% in other groups. As a whole, mean plant occurrence was unchanged (+0.1), so that disappearing mesophilous plants were replaced by xero-thermophilous ones. But 74 plants lost occurrences for only 55 gaining ground, which means that only a minority of plants took advantage of the new conditions, even within XT groups.

These percentages of spatial turnover may hide very different situations, as a plant was considered as spatially winner or loser whatever the rate of change. This is why the trend on flora composition towards xero-thermophilous species was more precisely assessed with the sums of occurrences and of Braun-Blanquet coefficients within groups (Figure 5).

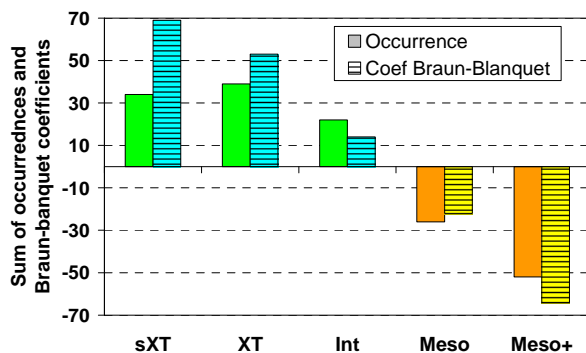
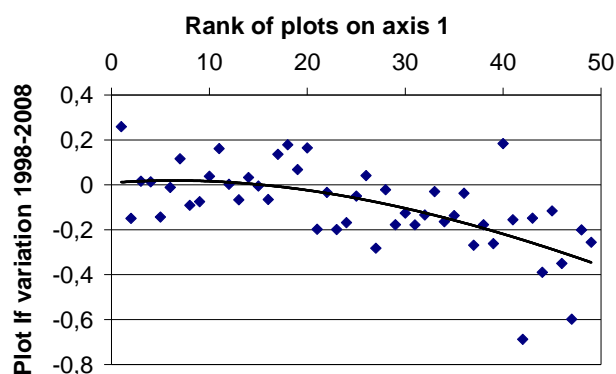


Figure 5: variations between 1996-98 and 2008 of the sums of occurrences and Braun-Blanquet coefficients per group in the 50 plots revisited in 2008. One occurrence = one species in one plot.



The sXT and XT groups together won 73 occurrences, corresponding to 1.5 plants per plot. But their sum of Braun-Blanquet coefficients won 122 points, nearly 2.5 points per plot. It means that not only new xero-thermophilous plants appeared in plots but also that some plants of these groups, already present in 1996-98, increased in dominance and cover. Meso+ and Meso plants lost together 68 occurrences and a bit more (86) in the sum of Braun-Blanquet coefficients, which means that, for these two groups, losses in cover percentage were mainly due to losses in occurrence. Globally the occurrence turnover between xero-thermophilous and mesophilous plants reached 3 plants, equivalent to 11.5 % in 10 years. Variations in the sum of Braun-Blanquet coefficients which are not explained by occurrence variations must be taken into account. When their equivalent in occurrences was added (0.6 occurrence for 1 points of coefficients), the total observed turnover excluding the intermediate group was close to 15 %.



This turnover between plant groups was not similar whatever the site. *Figure 6* shows that a biased turnover occurred mainly in mesophilous and intermediate sites, very dry and hot sites remaining more or less stable.

*Figure 6: If variation for the 50 plots resurveyed in 2008 according to their initial position on axis 1.*

### 3.4. Mapping Bi index on various scales

Bi index computed with global variables was mapped with a GIS software after being split into nine classes (*figure 7.a*). Each class included 1/9 of Bi total variation interval after exclusion of the 5% extreme values (2.5% at each end). These extreme values were merged with the first and last classes respectively. Range limits of various species match some of these classes. For example the darkest green (class 9) corresponds to the observed niche of Scots pine and related alpine and meso-European relict species, and excludes *Pinus halepensis* because of deep frost in winter. On average soil conditions and with a neutral topography, class 3 (orange) is the extreme limit of *Quercus pubescens*.

To show the evolution of potential vegetation, we computed and mapped Bi index (*figure 7b*) with the climate of year 2050 according to various scenarios: +2°C, -20% and -30% respectively for spring and summer rainfall, corresponding to the middle of the 21<sup>st</sup> century, with the same rainfall and just a bit hotter than the climate of the last decade.

## 4. Discussion

### 4.1. Validating and quantifying vegetation turnover

A 5 to 10% change in plant composition in the same plot between two following censuses, or with different survey methods, is common without any environmental change (Archaux et al., 2006; 2007). But in such a case this change is not related to a specific gradient, as plants within a given group replace each other. In this study, the most mesophilous and xero-thermophilous plants (Meso+ and sXT groups) were more concerned, respectively loosing and gaining more than intermediate ones. Meso and XT groups also showed a significantly unbalanced turnover.

The real turnover did not concern only the species at the very limit of species distribution for each plot. More distributed variations along the gradient give a lower If shift on axis one, but the same trend as far as species appear and disappear symmetrically. It may explain why the observed turnover was weaker than the simulated one. Although observed patterns of flora turnover were more complex than the simulated ones, they validate the method used for the simulation.

The observed trend is clearly biased towards heat and drought resistant plants. It is opposed to what is expected in aging forest structures. Indeed, in Southern Europe the Mediterranean ecosystems were transformed by several thousand years of disturbances and development (Blondel and Aronson, 1999). The natural evolution of the unmanaged stands of this study, most of them adult but far from senescence, should be a maturation process leading to an increasing dominance of mesophilous and shade tolerant plants and



the reduction of light demanding, generally xero-thermophilous species, inherited from past land uses (Tatoni and Roche, 1994). Probably, the adverse climate conditions in the last decade also contributed indirectly to a hotter and drier microclimate in the undergrowth, limiting canopy density through tree mortality (Allen et al., 2009), low branching rates and reduced leaf area (Thabeet et al., 2009, Girard et al., 2010).

The potential turnover (25%) simulated on plot scale in this study with the climate expected in the middle of the 21st century hold with previous studies on larger scales: Bakkenes et al (2002) showed that 32% of the European plant species that are present in a grid cell of a few square kilometres in 1990 should disappear from that cell before 2050. High rates of potential extinction among endemic species (average 11%, up to 43%) were forecasted by Malcolm et al. (2006) for the whole Mediterranean basin and other biodiversity hotspots in the world by 2100.

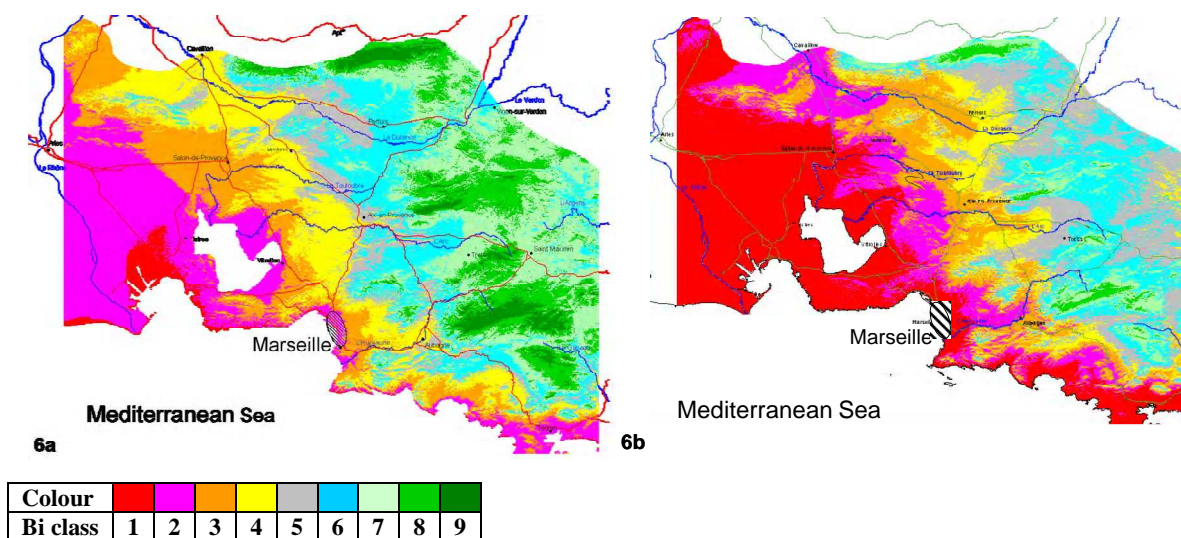


Figure 7: Bioclimatic index (Bi) computed with global variables and mapped on regional scale with ArcGis® software in 9 classes of equal Bi index span. The darkest green (class 9) corresponds to the potential niche of Scots pine and related alpine and meso-European relict species. The three shades of green together draw the area of the supra-Mediterranean bioclimate, the blue to pink intermediate colors the meso-Mediterranean and the red the thermo-Mediterranean bioclimate (Emberger, 1930).

7a: Map with 1961-96 mean climate.

7b: Map with 2050 climate (IPCC, B2 Scenario). Relict vegetation has no potential niche left in the study area. *Q. pubescens* should move away far from the coast, and the growth of *P. halepensis* been slower in most of the study area.

#### 4.2. Flora resistance on landscape and local scales

Plant composition turnover observed in the last decade was significant but not as considerable as simulated by the model. A resistance to climate variations was observed, which may be partly explained by landscape structure. Bi index mapped at any scale is laid out like a patchwork of fragmented bioclimatic classes. When topography and soil are added on local scale, six among the nine classes represented on regional scales with medium site conditions can be found on a single square kilometre of hilly landscape with steep slopes and only one or two hundred meters of difference in elevation. Thanks to that fine grain mosaic, xero-thermophilous plants are scattered everywhere even at high elevation, taking advantage of steep south-facing slopes, shallow and rocky soils. Most of the time, some of them simply remain from degraded ecosystems inherited from former land uses and fires. They are ready to sprawl from these positions in presently cold and wet areas when mesophilous species become less competitive because of climate change. Mesophilous species are supposed survive, in dry and hot areas, in scattered niches combining cool expositions, deep soils and favourable topography. Even when killed by extreme climate events, they may come back by seed dispersal from refuges and long lifespan soil seed-banks (Zobel et al., 2007). However, such a hypothesis is not fully supported by our results. The best soil and topographic conditions proved to

be no longer sufficient to compensate the climatic water stress in recent years, leading to the extensive dieback of mesophilous species in good sites. As an example among forest trees and representatives of middle-european relict species, *Pinus silvestris* L., although limited to the highest elevations and north slopes, paid an heavy toll to 2003 scorching heat and following drought (Thabeet et al., 2009). In the future, the increase in water stress should lead this compensation limit to shift left along axis one, and the turnover to start even in the driest and hottest sites of the study area.

### 4.3. Management issues

Several reserves try to protect Alpine or middle-European flora in Mediterranean mountains. But protected areas are generally fragmented and scattered in developed lands. Corridors are lacking to allow species to move from one to another. This is why it would be necessary to include public and private multi-use lands in conservation practices (Heller & Zavaleta 2009) and to look for the parts of these human-dominated landscapes that should be suitable for forest species. Bioclimatic maps like *figure 7*, if regularly updated, could help designing such strategies.

However, many of the small isolated areas of relict vegetation should be kicked out by the top. According to Trivedi et al. (2008a) 70 to 80% of plant species in similar low mountain conditions should lose most of their potential niche in the next decades, as shown in *figure 7.b* for *Pinus silvestris* and associated flora. Moreover, large scale approaches may underestimate this potential climate-based disappearance by far. Extreme weather events may cause larger gaps in already scattered populations (Opdam and Wascher, 2004) and drive them below the critical level of metapopulation persistence. So that *ex-situ* conservation of endemic and rare species or genetic resources should be urgently implemented. For example, *Pinus silvestris* in Provence at low elevation proved to be far more resistant to drought than most other origins of this species. This resource could be useful in the future at higher latitudes, and for genetic improvement programs. But most of the concerned stands were killed between 2003 and 2007 and the last ones should soon be lost.

## 5. Conclusion

Combined with exceptionally high temperatures, repeated droughts between 1998 and 2008 severely impacted vegetation in south-eastern France. This unexpected experience allowed assessing, three decades sooner, the consequences of the climate forecasted as normal in the future.

We showed that a rapid turnover occurred in ten years on site scale. It was surprisingly faster in the most favourable sites, where mesophilous species could not survive. It may concern all the study area in the future. Accordingly, the simulations with a bioclimatic model forecasted even more extensive changes with the climate of the last decade. Whatever the quality of models, the long term follow-up of permanent plots is irreplaceable to understand and measure the impact of climate change.

As climate change may accelerate in the future, conservation policies for rare and endangered species, and more generally conservation policies based on fixed reserve networks, should be reconsidered. It is particularly relevant in low mountains where the trailing edge of ecological niches for these species should soon reach the highest ridges.

Landscape structure at a scale fitting with a detailed assessment of topographic and soil variables allows an operational assessment of the change in plant composition and the shift in plant future distribution. Taking into account seed dissemination distances may improve such an assessment, as the scales are of the same order. Many parameters including the real species migration capacity, population dynamics, biotic interactions and community ecology should be included in models (Brooker et al., 2007; Guisan & Thuiller, 2005) to improve the spatial assessment of plant migration in landscapes.

Therefore, such assessments on an operational scale should be multiplied in the main ecosystems and regions, so that large scale approaches could be corrected and better interpreted. Small scale approaches, tailored to specific needs, also enhance local knowledge and encourage dissemination and decision making at operational forest management level. Ecological as well as economical issues are at stake.

## Acknowledgements

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## **Annex 1: statistical procedures**

We used a classical unweighted CA analysis with Braun-Blanquet coefficients to obtain the Flora index as the coordinates of plots on the first CA axis. We checked the robustness of the CA axes towards potential inaccuracies of floristic censuses due to time or spatial strategies or the observer (Archaux et al., 2007; Archaux et al., 2006) and towards analyses options. This verification was performed with a Multiple Factorial Analysis (MFA) (Escofier and Pages, 1994) testing the stability of CA axes and plots coordinates: on one hand by increasing the number of plots where a plant must be present to be taken into account from 3 to 30, on the other hand comparing presence/absence and Braun-Blanquet coefficients in the analysis. CA axes 1 to 3 and plots coordinates proved to be particularly stable ( $r^2$  of plot rank on axis 1 > 98%) whatever the code used (BB coefficients or presence/absence) and up to a limit of 25 occurrences for plant selection.

Some variables seemed to have non-linear relationship with the Flora index (Fi). To optimize the PLS model, we first checked the relation pattern of all relevant variables with Fi using neural networks and transformed some of them (log, sigmoidal or polynomial). Neural networks were used combining variables 6 by 6. Each neural network was optimized with a 200 replications bootstrap, each replication including  $10^4$  calibration steps. After the optimization of the neural network, the response of each variable was plotted on its whole variation interval, the other variables being maintained at their mean value if they were not correlated with the tested one, or maintained successively to their first, second and third quartile for those which were correlated.

In the last case, the 3 responses were combined in a sliding weighted mean to obtain the global response. We only transformed a variable according to non-linear relation showed by neural networks when this relation was stable throughout these many tests and enhanced as well (i) the weight of the variable in the neural network optimization and (ii) its partial correlation coefficient or the total explained variance in the PLS regression.

For the choice of relevant variables in the model, we used an ascending and descending stepwise PLS regression validated at each step by a permutation test on PLS components and a cross-validation for concerned variables. All variables in the final version of the model were highly significant on the first two PLS components ( $p < 0.001$ ). The number of significant components for PLS regression was chosen with a 10,000 replications permutation test on observations (Good, 1994), keeping components which percentage of explained variance was not passed by more than 5 % of the permutations. With significant components, variables were sorted through a 1,000 resampling cross-validation test (Amato and Vinzi, 2003); only variables which confidence interval (95%) for the partial correlation coefficient excluded 0 were used.

We used ADE4 software (Thioulouse et al., 1997) for CA and related operations (introducing supplementary observations and variables), for MFA and PLS permutation tests, Statgraphics® software for stepwise PLS regression, R software (R\_Development\_Core\_Team, 2004) for the cross-validation of PLS variables, and PPPhalos software (Guiot, 1991) for neural networks.