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A few prospective ideas on climate reconstruction: from a statistical single proxy approach towards a multi-proxy and dynamical approach

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Abstract

Important progresses in palaeoclimatological studies have been made using statistical methods. But they are in somewhere limited as they take the present as an absolute reference. The availability of mechanistic models to simulate the proxies measured in the sediment cores gives now the possibility to relax this constraint. In particular, vegetation models provide outputs comparable to pollen data. We present the evolution of the mechanistic approach based on model inversion with several examples where models are progressively more sophisticated (from an equilibrium BIOME3 model to a dynamic LPJ-GUESS model). We show also how it is possible to take into account several proxies measured on the same core (lake-level status and δ^{13} C) when they are related to a component of the vegetation. Examples presented concern Last Glacial Maximum in Europe and Africa, Holocene in a site of the Swiss Jura, an Eemian site in France. The main results are that: (1) pollen alone is not able to provide exhaustive information on precipitation, (2) assuming past CO₂ equivalent to modern one may induce biases in climate reconstruction, (3) vegetation models seem to be too much constrained by temperature relative to precipitation in temperate regions.

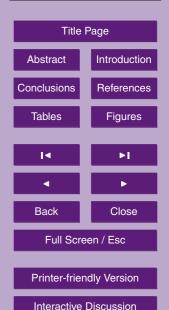
1 Introduction

For a long time, Quaternary paleoecologists have used intuitive methods to reconstruct paleoclimates or paleoenvironments from biological data. The most common approach has been to compare the present-day distribution of selected species with the corresponding distribution of climate variables thought to be determinant for the distribution of the selected species. The species are analyzed separately and related to one climatic variable. But the species respond to a combination of climatic variables and their distribution is controlled by different climatic factors in different parts of their ranges. Moreover, climate parameters are often interrelated. Thus, it has been necessary to develop methods taking into account the ecological complexity of species and

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assemblages, and of their relationships with climatic factors. Several species are simultaneously compared to the distribution of several climatic variables (Iversen, 1944; Atkinson et al., 1987).

Pollen data provide not only presence/absence of species but also their relative abudances and it is possible to develop response models where the abundance of the species is expressed as a function of the climate (Bartlein and Prentice, 1986). These statistical models are only valid on climatic niches presently realized and their extrapolation to the past could be problematic (Guiot et al., 2008). Moreover, to reconstruct climate, it is necessary to inverse these response models, and it cannot be achieved directly. Usually one calculates backward statistical relationships between climate and species. These relationships are called transfer functions. They are based on a few assumptions:

(1) Climate is the ultimate cause of changes in the paleobiological data.

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- (2) The ecological properties of the species considered has not changed between the period analyzed and the present time, and the relationship between the species and the climate is thus uniform through time.
- (3) The modern observations contain all the necessary information to interpret the fossil data.

The second and third assumptions originate from the uniformatarian principle. It is implicit in most paleoecological studies, but constitutes an unprovable premise, especially when going back in time in the geological archives. The second assumption is sometimes far to be fulfilled. While polar ice core records have shown that the atmospheric $\rm CO_2$ concentration has fluctuated significantly over at least the past 740 000 yr (EPICA, 2004), a number of physiological and palaeoecological studies (e.g. Jolly and Haxeltine, 1997; Cowling and Sykes, 1999) have proved that plant-climate interactions are sensitive to the atmospheric $\rm CO_2$ concentration. $\rm CO_2$ effect can only be taken into account with mechanistic models validated with experimental data.

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Moreover, pollen data does not contain all the information of the climate in a given site, either because pollen is an approximative image of the vegetation covering the site (image disturbed by pollen grain transportation and by the fact that a pollen taxon is not a univocal species), or because all species are not all affected by the same climatic variables. Herbaceous vegetation is not really controlled by the winter conditions and Prentice et al. (1992a) have shown that, in a Mediterreanean site, a forest could have been replaced by a dry steppe during the glacial period while lakes recorded as much as water than in present. Their simulations have shown that a more abundant winter precipitation increases the run-off and is not available in spring and summer for vegetation. We then need several complementary proxies to decipher the complex seasonal climate. In this multi-proxy approach also, mechanistic models are of a great help to deal with an integrated view of the ecosystem.

The objective of this paper is to show how it has been possible to take into account progressively more complex processes using vegetation models: from the equilbrium model BIOME3 (Haxeltine and Prentice, 1996) to a dynamic vegetation model LPJ-GUESS (Smith et al., 2001). In parallel the use of a single proxy (pollen data) has been completed by lake levels data and by isotopic data, both proxies giving information on different aspects of the climate. We will also conclude on the directions that paleoclimatology should follow to fully exploit the increasely diverse and improved set of archives and proxies.

2 Pollen and equilibrium vegetation model

A pollen spectrum is assumed to reflect the composition and structure of the regional vegetation, and then can be correlated with net primary production (NPP) of various plant functional types (PFT, i.e. groups of plant species of similar characteristics and responding in a similar way to climate). The pollen taxon percentages are also grouped in PFT (pollen PFT scores) as defined by Prentice et al. (1996).

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The model used is a modified version of BIOME3 (Haxeltine and Prentice, 1996). It is a process-based terrestrial biosphere model which includes a photosynthesis scheme that simulates acclimation of plants to changed atmospheric CO₂ by optimisation of nitrogen allocation to foliage and by accounting for the effects of CO₂ on net assimilation, 5 stomatal conductance, leaf area index (LAI) and ecosystem water balance. It assumes that there is no nitrogen limitation. The inputs of the model are soil texture, CO₂ rate, absolute minimum temperature (Tmin), monthly mean temperature (T), monthly total precipitation (P) and monthly mean sunshsine (S) i.e. the ratio between the actual number of hours with sunshine over the potential number (with no clouds). From these input variables, the model computes bioclimatic variables. Then, the model calculates the maximum sustainable leaf area index and the NPP (in kg m⁻² yr⁻¹) for the PFT's able to live in such an input climate. Competition among PFT's is simulated by using the optimal NPP of each PFT as an index of competitiveness. The most important PFT in Europe are: temperate broadleaved evergreen trees (tbe), temperate summergreen trees (ts), temperate evergreen conifer trees (tc), boreal evergreen trees (bec), boreal deciduous trees (bs), temperate grass (tg), woody desert plant type (wd), tundra shrub type (tus), cold herbaceous type (clg), lichen/forb type (lf). The pollen PFT's are slightly different in such a way that some of these PFT's are sometimes subdivided.

2.1 Europe at the last glacial maximum

As a vegetation model is oriented, from climate to vegetation, its use for climate reconstruction requires to inverse it. Technically the inversion consists in finding the value of an input climate parameter for which the model output fits as well as possible the observation. The input vector of climate parameters must be reduced to a small number of representative variables (Tjan, Tjul, Pjan, Pjul), from which all the other climatic variables are deduced (details in Guiot et al., 2000). To provide a comparison between sites and times, climate variables are expressed as "anomalies" or δ climate, i.e. differences between proposed climate and the modern climate at the considered site. The measure of fit between the vegetation model outputs (NPP) and the observations

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(pollen PFT scores) is called the likelihood. The likelihood is built using a modern dataset of pollen samples and vegetation simulated using the modern-known-climate. In Guiot et al. (2000) the likelihood is the sum of square distances between transformed NPP using an artificial neural network and observed pollen PFT scores.

Finding the "best" climate of a pollen sample can be achieved using an optimisation algorithm to minimise the distance – given by the likelihood – between simulated vegetation and pollen by changing the climate input. As we are more interested in finding a range (or distribution) of possible climate, it is preferable to adopt the Bayesian paradigm Robert (2001). This paradigm creates and links the concepts of prior and posterior information through the likelihood. The prior information is the information available on climate before analysing a specific pollen sample. It is described by a distribution of the climate variables. Roughly, the posterior distribution is obtained by measuring the fit – using the likelihood – of the vegetation simulated from the climate prior. Thus, the posterior combines information about the prior on climate, the vegetation model and the data.

Since the early 90's Bayesian statistics are accompanied by inference algorithms (Robert and Casella, 1999) which allow to perform posteriors computation. These algorithms – coherently with the Bayesian inference – provide an integration over the climate parameter space instead of an optimisation. A popular type of such algorithms is known as Monte Carlo Markov Chain (MCMC) algorithm. Let us consider a multi-dimensional mathematical space where each dimension represents a climate parameter range. A vector of parameters is an element of the multi-dimensional climate space. The Metropolis-Hastings algorithm is an iterative method which browses the climate space according to an acceptance-rejection rule (Metropolis et al., 1953; Hastings, 1970). The output of this algorithm is a "path" or "chain" of climate parameters describing the posterior distribution of climate parameter.

The method has been applied to 15 Last Glacial Maximum (LGM, considered there as the period between 23 and 19 ka BP) sites in Europe. The reconstructions are given as probability distribution histograms. Each site is sorted according to its lati-

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tude (Fig. 1). The first experiment is done with a high level of CO₂ (340 ppmv) close to the atmospheric concentration existing during the modern data sampling. Annual temperature shows an increased gradient from the southernmost site (about 35° N) towards the northernmost (48° N), and, for the annual precipitation, a decreased gradient. It is 0.81±0.35°C for temperature and -29±12 mm/yr for precipitation. It means that a larger temperature decrease of temperature in the south than in the north is necessary to transform forest into steppes and, in the north, a stronger precipitation decrease is necessary. When the LGM level of CO₂ is applied, the gradients become unsignificant for both variables. That means that CO₂ lowering is enough to reduce forest. There is then a real bias in ignoring the true level of CO₂ for climate reconstruction (when statistical methods are used instead mechanistic models). This bias reach 3°C in southernmost sites and about 1°C in nothernmost ones, meaning that CO₂ becomes limiting far from the ice cap where temperature is not too limiting.

2.2 Eurasia and Africa at the LGM

Wu et al. (2007a) have improved the method. First BIOME3 has been replaced by BIOME4 (Kaplan et al., 2003). Second, the bijective relationship between model simulations (NPP) and pollen PFT scores has been replaced by a transfer matrix between the model PFT's and the biome scores calculated from pollen. This matrix is an empirical result based on modern data and theoretical definition of the biomes. The method has been applied to a continental scale: Eurasia and Africa.

The estimated anomalies of the climatic parameters for the LGM period are shown in Fig. 2. The left part of the graphics concerns Africa. There is a large dispersion which can mainly be explained by a large dispersion of elevation. Wu et al. (2007a) have shown a strong gradient of precipitation function of elevation. For the modern level of CO_2 , we cannot it a linear relationship of temperature to latitude in Africa, but yet in Europe, the relationship is negative: high latitude sites had a temperature anomaly of about $-12^{\circ}C$ and southern sites were $5-10^{\circ}C$ colder. The gradient is negative instead of positive in Fig. 1. It is mainly due to the better ability of the model to simulate the

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LGM vegetation, which is intermediate between cool steppes and tundra. A biome called steppe-tundra has been introduced in BIOME4, which fits then much better to the data.

At low CO₂ concentration, the relationship according to elevation is not significantly different from the high level relationship. Moreover the reconstructed anomalies under low level of CO₂ are not significantly different from the high level ones. Wu et al. (2007a) had found a clear bias of MTCO due to CO₂ (about 10°C) but not for MTWA (there is no clear pattern). The annual temperature seems then behaviour more like summer temperatures. For Mediterranean sites, annual temperatures seem rather higher under low CO₂.

In Africa, temperature was not very different from present values. Precipitation has a much more structured profile. Under high CO_2 , anomalies were close to zero in South Africa and between -1000 and 0 mm/yr at equator, depending on the elevation. Under low concentration, the reconstruction in the southern part of the continent was similar, and in the central part, the dispersion is higher: -1200 to 0 mm/yr. For high altitude sites (>1500 m), the precipitation mode for 340 ppmv was at about 1000 mm/year and is replaced by a large double peak from 1100 to 700 mm/year. The disappearance of forest above 2000 m elevation can then be explained partly by a precipitation decrease and a CO_2 lowering (Wu et al., 2007b). In fact, by looking at the variable α closely related to the stomatal area and the water use efficiency, Wu et al. (2007a) found that the mode located in [-40, -28%] increases, with lowering CO_2 , to [-40, -8%]. The dominating factor is then clearly that an oversetting of CO_2 to 340 ppmv induces an overestimation of the water stress.

Several solutions are possible for the LGM climate in regions where a mixture of steppes and tundra existed. As these biomes have no clear analogues today, a reconstruction based on statistical methods will tend to choose the least poor match, or fail to find a match (Peyron et al., 1998; Jost et al., 2005). With statistical methods, these analogues were located in tundra or very cold steppes, resulting in very low reconstructed temperatures. By using a mechanistic model and probability distributions,

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the results are multi-modal and the most probable mode is different according to the CO₂ concentration. All possible solutions at LGM CO₂ levels can be explored. Complementary proxies are, in this case, of great help to precise the best suitable solution.

3 Lake levels and an equilibrium vegetation model

The palaeo-lake Le Locle (47°03′ N, 6°43′ E) has been dried at the last century. It is located at 915 m a.s.l. in the high Swiss Jura. The pollen and lake-level data used in this study were obtained are described in Magny et al. (2001). Lake levels curve indicates that the Younger Dryas (YD) was characterized by a trend toward a lake-level lowering and strong instability (Fig. 3). The early Holocene had three major phases of low levels, before 10 ka BP and between 9 and 8.5 ka BP, and after 7 ka BP. Concerning the vegetation history (represented by the deciduous trees curve and the total of tree pollen (Fig. 3), the Younger Dryas was characterized by rather large percentages of trees (*Pinus, Betula*) together with about 10% of *Artemisia*. Early Holocene was characterized by an increase of *Corylus*, then *Ulmus* and *Quercus*. Nothing in the vegetation history can be related to the rise in lake level at ca. 8400–8300 cal yr B.P.

We apply first the same method as in Sect. 2.1, pollen being used alone to constrain the model and CO₂ assumed to be constant and equal to the pre-industrial value 280 ppm. The prior distribution for January and July temperature is uniform between –8 and +4°C (in anomalies) and for precipitation, between –40 and +40% of modern conditions. We call it "experiment pollen" (ExP) (Fig. 4). YD is characterised by a temperature lower than present by 8°C. Annual Precipitation does not seem to have any trend. The second experiment (pollen-CO₂, ExPC) is obtained by providing to the model the atmopsheric CO₂ as reconstructed from the Taylor Dome ice core (Indermühle et al., 1999) (Fig. 4). It has the largest effect on the reconstruction of temperature – an anomaly of 5°C instead an anomaly of 3°C with ExP – when its concentration is the lowest. This is enlightened by the differences ExPC-ExP between probability distributions of ExPC and that of ExP: the modes of ExP (in blue) are systematically lower than

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the modes of ExPC (in red). As for the LGM, this shows that not taking into account the true value of CO₂ induces a bias in the temperature reconstruction, the effect being maximum during the YD. The effect on precipitation seems to be negligible (the blue and red distributions being flat and not contrasted).

The last experiment (pollen- CO_2 -lakes, ExPCL) is obtained by constraining the model with pollen, CO_2 and lake-levels (Fig. 4). To deal with lake-levels, we compare, for each iteration the lake-levels with the precipitation minus evapotranspiration (P-E), closely related to run-off. Both quantities are substracted by their modern value at the study site. We call ΔL , the anomaly of lake-level and $\Delta (P-E)$ the anomaly of P-E. Are eliminated the cases where

$$(|\Delta L| \le 0.5)$$
 and $(|\Delta (P - E)| > 200 \,\text{mm})$
 $(\Delta L > 0.5)$ and $(\Delta (P - E) < -100 \,\text{mm})$
 $(\Delta L < -0.5)$ and $(\Delta (P - E) > 100 \,\text{mm})$ (1)

Figure 4 shows that the variations of temperatures do not change, but the variations of precipitation follow much better those of the lake levels, with also a decrease of the uncertainties (indicated by a narrowing of the probability distribution). The probability distribution differences (ExPCL-ExP) shows that ExPCL distributions are narrower than the ExP modes (blue areas on both sides of the red area indicate large distributions). So when pollen is used alone, the precipitation reconstruction have a much larger uncertainty.

These experiments prove again then that ${\rm CO_2}$ must be taken into account at least during periods where it is low. Another point is that precipitation, in temperate regions (at least), can not be inferred with a sufficient confidence from vegetation proxies only. Vegetation uses a part of precipitation falling on the ecosystems, a significant part runs off and consequently, a complementary proxy is needed to infer correctly the total amount of water available within the ecosystem.

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4 δ^{13} C proxy and equilibrium vegetation model

The procedure used is based on BIOME4 model (as in Sect. 2.2) the likelihood function used to measure the similarity between model outputs and data is

$$LH = -\frac{(\delta^{13}C_o - \delta^{13}C_s)^2}{S^2}$$
 (2)

where subscripts o and s correspond to target and simulated values, respectively and where $1/S^2$ is the whole model precision. It is an adjustable number which measures the quality of the fit between model outputs and data. When biomes estimated from pollen data are available, it is possible to use this information to make an additional selection of the runs. If the simulated matches with data, the iteration is kept, if not, it is rejected. Hatté et al. (2008) have compared the results obtained with biome alone (which is a single pollen approach) and with carbon isotopes constrained by pollen biomes. The method is validated in Hatté et al. (2008). We reproduce here the results obtained for La Grande Pile sequence.

La Grande Pile is located at 47°44′ N, 6°30′ E, 330 m a.s.l. with annual precipitation of 1080 mm and a mean annual temperature of 9.5°C with a seasonal range of about 18°C between the warmest and the coldest months. The GPXXI core has been taken at the Grande Pile site at the same time as those investigated by Woillard (1978). The data are presented in Rousseau et al. (2006) and concerns the Eemian period (130 to 110 ka BP).

For each level of the La Grande Pile, an input vector was defined which defines (1) the δ^{13} C of the sample, (2) the target biomes as the two with the highest scores achieved by the biomisation procedure (further information in Rousseau et al., 2006), (3) the atmospheric CO₂ concentration based on Petit et al. (1999) record interpolated at La Grande Pile time-scale and (4) soil type and texture. The reconstructed annual temperature and precipitation are based on a threshold of –0.5 for LH function, meaning an accepted error of –0.7‰ for δ^{13} C.

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Mean annual temperature and annual precipitation reconstructed by inverse modelling constrained by biome(s) and δ^{13} C are there presented bracketed by the ranges which should be obtained by pollen biome constrains alone (Fig. 5). The added-value of double constraints is particularly true for precipitation reconstruction: single constraints infers a constant value with large uncertainties ([-600,+200 mm/yr] in precipitation anomaly) and double contraints decrease uncertainty by 2 to 4. Furthermore, reconstructed temperature ranges are often decreased by a factor 2. This confirms the conclusion of previous section that pollen alone cannot give a sufficiently precise reconstruction of precipitation. This shows also that the use of two proxies decrease the uncertainty on reconstruction of both variables and inverse modelling is an elegant way to integrate several proxies at the conditions that they are related to vegetation.

5 Dynamic vegetation model

LPJ-GUESS is an noticeable improvement of BIOME4 as the dynamics of the vegetation stands is taken into account. A full description of the model can be found in Smith et al. (2001). In LPJ-GUESS, cohorts of trees of different species, age and structure compete for light and soil resources on a number of replicated patches of plants. Either PFT (Sitch et al., 2003) or species (Hickler et al., 2004) may be simulated. Garreta et al. (2008) used the species version which includes 18 species. LPJ-GUESS has standard inputs, i.e. with monthly values of precipitation, temperature and cloudiness. For each study site, past and present, precipitation and temperature chronologies were interpolated from the CRU TS 1.2 dataset (New et al., 2002), which has a spatial resolution of 10'. For cloudiness they fitted a relationship between monthly cloudiness and both monthly precipitation and temperature per site. The monthly temperature and precipitation were deduced from a 6-dimensional climate parameter vector: $C = (T_{\text{Jan}}, T_{\text{Jul}}, P_{\text{win}}, P_{\text{sum}}, P_{\text{aut}})$. The first two variables are temperature anomalies (in °C) from January and July for 1901–2000. The four other ones were seasonal (winter, spring, summer and autumn) precipitation relative anomalies (in %).

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Pollen taxa used are 14 arboreal taxa (*Abies, Alnus, Betula, Carpinus, Corylus, Fagus, Fraxinus, Picea, Pinus*, evergreen *Quercus*, deciduous *Quercus, Tilia, Ulmus* and *Populus*) and a 15th herbaceous taxon (GrSh, summing all the herbaceous taxa) were taken. This choice has the maximum of coherency with the 18 species defined in LPJ-GUESS. Garreta et al. (2008) applied their method to a fossile core (Meerfelder maar, Litt et al. (2008), but we just present here the validation of the method with modern samples.

The inversion procedure is rather different from the procedure used in the previous sections because the LPJ-GUESS model is a stochastic model (not BIOME4) and the MCMC algorithms do not apply to that situation. Stochasticity of the model means that, when the model is run twice, the simulations are not exactly the same. The inversion uses the particle filter algorithm or sequential Monte-Carlo algorithm (Doucet et al., 2001). A major difference with previous attempts is that the temporal structure of the pollen series is taken into account.

To simulate vegetation at time $t_j > t_i$, with t_i and t_j consecutive time periods (corresponding to the resolution of the core), the vegetation model starts with V_{t_i} and runs for $t_j - t_i$ years. If $t_j - t_i$ is short, vegetation simulated at t_j is strongly forced by vegetation V_{t_i} and then, implicitly, by climate C_{t_i} . This constraint gives a time-coherence to vegetation and then to reconstructed climate, and helps to produce "histories" or "dynamics" or joint distributions of vegetation and climate. This constraint can be seen as a filter which smooths the local bias of independent reconstructions.

A key element of the inversion model is the relationship between simulated vegetation and pollen data. In the previous sections, this has been either calculated with a statistical non linear relationship or with a transfer matrix. Here it is approximated by a kernel surface (or a response surface) where the pollen taxon is expressed as a function of the taxonomically closest model taxon. This kernel was calibrated on a dataset of 1209 surface samples covering Europe and North Africa. It is illustrated for *Alnus* (Fig. 6) where the maximum weight is found where the coherency is best between data and model (here, for low pollen values and low NPP and for pollen values of 0 and NPP

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around 0.02).

The results of the method are shown as (smoothed) posterior distributions of each climatic variable. It is illustrated for an Andalucian site (Fig. 7). Mean discrepancies between posterior medians and expected values of the 6 reconstructed parameters are negligible by comparison with interval widths: the differences between the modes are <5°C for temperature and close to 0% for precipitation. This kind of analysis has not really a sense for a single site. To really evaluate the biases, it is necessary to repeat this validation for several sites. It has been done for 30 sites in Europa where ? have shown that the mean bias was <1°C and 3% in absolute value. Thus, the method seems to be unbiased.

To provide a valuable information, the posterior distributions must be narrower than the prior ones. It is the case for temperature where the lower limit of temperature distribution goes from -15° C to -5° C in January and from -10° C to -6° C in July (Fig. 7). Precipitation posteriors are not narrower than their priors, a result which show that improvements are still necessary. Most of them should be done in a better modelling of the relationship between pollen dispersion and plant productivity.

6 Conclusions

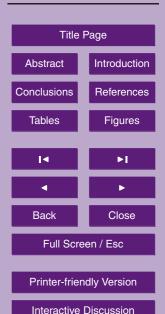
This paper has shown progresses which have been made in the last ten years to relax the uniformatarian hypothesis which is behind most of the paleoclimatological studies.

This hypothesis says that we may find in the modern world, similarities for the past and then explain the past in one location as a realization of a present situation somewhere else in the world. This is clearly the basis of the analogue approaches, but also of all statistical approaches based on a modern dataset considered as a training dataset (regression based methods, artificial neural networks ...). Mechanistic models able to simulate a proxy in function of climate give us the chance to work around this hypothesis at the condition that such models were strongly based on mechanisms and not only a set of linear or non linear equations calibrated on modern datasets. Vegetation

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models is among this category.

Pollen data have the chance that vegetation models based on physiological laws have been developed more than fifteen years ago (Prentice et al., 1992b). Having such model available is not the only condition. These models must also be enough simple to work with accessible inputs (climate, soil structure ...). It has been the leading mind of most of the vegetation models developed since this pioneer work. This paper has shown how to goes from a relatively simple equilibrium model (BIOME3) to a dynamic model as LPJ-GUESS. These models give the possibility to work under conditions very different from the modern ones. It is clearly the case for the atmospheric CO₂ concentration often lower than the continuously increasing present one (200 ppmv during the glacial periods, around 280 ppmv during the interglacials and more than 360 ppmv today). The seasonality changes are also an interesting point. It is induced by variations of earth orbit around the sun (see the pioneer work of Berger, 1978). This feature is implicitly taken into account, at least through its effect on temperature and precipitation, by the inversion procedure as different priors are set for winter and summer.

Vegetation models are an elegant solution to integrate several proxies. They simulates quantities which may be related to pollen data. They simulate also fractionation of $\delta^{13}\mathrm{C}$ in the plant which can be compared with isotopic measurements in the sediment bulk. They simulate also water absorbed by the plant and water running off. The runoff, represented by precipitation minus evapotranspiration, can be directly compared to lake-levels data when the core is lacustrine. As often lake recharge is done in winter and water useful for vegetation in spring or summer, the use of both proxies give a complementary enlightening of two complementary aspects of the climate, which enables also to study various seasonalities.

Concerning the main results, we may drawn several important points:

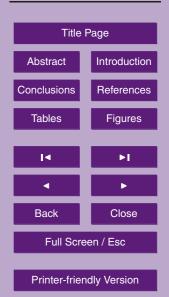
1) There may be a significant bias in not taking into account the difference of CO₂ between modern level and past levels. Particularly, during the glacial periods where the difference is maximum, CO₂ fall is partly responsible of the destruction of for-

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est in Mediterranean area during the LGM. Not taking it into account, the results tend to attribute it to a too important temperature fall. The tundra-steppe vegetation of central and southern Europe is interpreted as a tundra vegetation when statistical methods are used, while a mechanistic model as BIOME4 interpret it as a cool steppe, less cold than the tundra, especially in summer. Some biases can also exist during less cold periods (Younger Dryas and even Holocene).

- 2) The use of lake-levels to constrain the reconstruction from pollen data reduces the uncertainty associated with the fact that pollen in temperate zones is a temperature indicator rather a precipitation proxy. The results, using Lake Le Locle pollen and lake levels proxies, have shown that, not only uncertainty is reduced but also larger variations are reconstructed across the Holocene.
- 3) δ^{13} C is another proxy strongly related to precipitation. The results on the Grande Pile Eemian have confirmed that the joined use of pollen and carbon isotopes reduces also the uncertainties on precipitation reconstruction.
- 4) The use of a dynamics model confirms the main role of temperature in the vegetation shifts in Europe. This approach is still in development and some improvements are necessary to make the method fully operationnal. A first result here, which maybe confirms points 2 and 3 above, is that the effect of precipitation seems to be underestimated in LPJ-GUESS or BIOME4.

Despite these points, this inverse vegetation modelling approach is not the panacea. First, because it is a model-based approach it is highly dependent on the quality of the vegetation model. Second, it requires a great deal of computation time, which will increasingly become a problem in adapting the technique to more sophisticated models. Third, the outputs of the model are not directly comparable with the pollen data without a pollen dispersion modelling. Further verification is required by adapting this approach to other vegetation models. It remains important, however, to use this approach in parallel with statistical approaches. The comparison of results is a major key in understanding relationships between paleoclimates and palaeovegetation.

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Finally, as A. Berger frequently claimed (personal communication), it is only after we will build an integrated model of the pollen accumulation in the core that real progresses will be achieved: this model should include all the processes such as vegetation development, pollen dispersion, catchment basin erosion, sediment accumulation.

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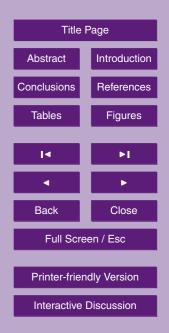


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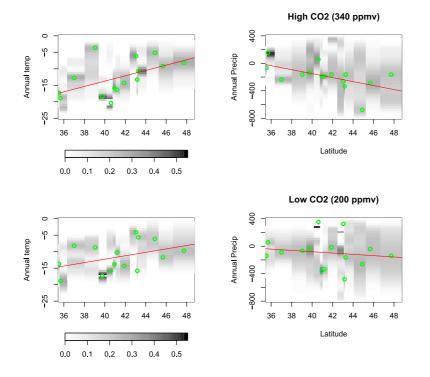


Fig. 1. Annual temperature and precipitation anomalies (i.e. deviations form present value) at the Last Glacial Maximum (21 ka BP) in function of latitude. The region covered is Europe. The graphic is based on 15 sites sorted by latitude. The grey scale indicates the probability distribution, the blue circles show the mode of the distribution and the red line the linear relationship between the mode and the latitude.

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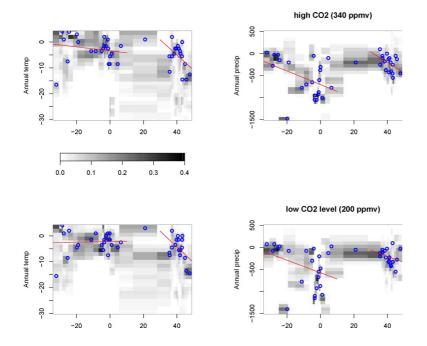


Fig. 2. Annual temperature and precipitation anomalies (i.e. deviations form present value) at the Last Glacial Maximum (21 ka BP) in function of latitude. The regions covered are Europe and Africa. The graphic is based on 42 sites sorted by latitude. The grey scale indicates the probability distribution, the blue circles show the mode of the distribution and the red line the linear relationships between the mode and the latitude, one for sites south of 10° N and one for sites north of 30° N.

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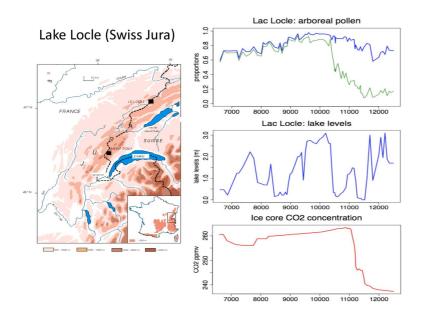
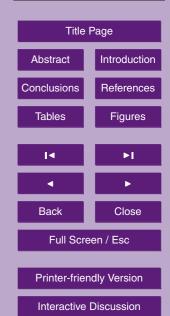


Fig. 3. Location of Lake Le Locle in Swiss Jura. The upper right graphic represent the proportion of tree pollen and the proportion of deciduous tree pollen in the pollen diagram. The middle right graphic represents the lake-levels. the lower right graphic represents the CO₂ concentration in the ice core bubbles of Taylor Dome (Indermühle et al., 1999). Time scales are in calibrated years BP.

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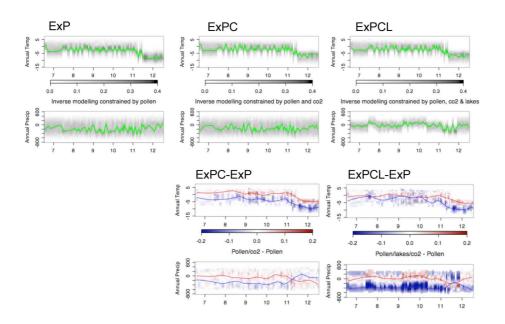


Fig. 4. Results of three experiments on Lake Le Locle. Two variables are constructed, annual temperature and precipitation. Grey sale indicates the probability distributions. The green curve indicates the modal curves. ExP show the results when pollen alone is used with inverse modelling; ExPC when pollen is used with the Taylor Dome CO₂ concentraton; ExPCL, when pollen is used with Taylor Dome CO₂ and with the lake levels constraints. The "blue/red" graphic represent the difference between probability distribution of two experiments. The curves represents the modal curves.

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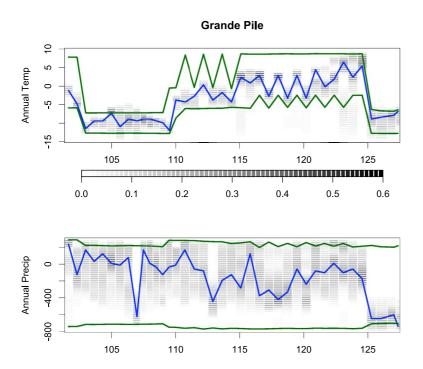


Fig. 5. Temperature and Precipitation reconstruction at La Grande Pile during Eemian period. Mean annual temperature and annual precipitation reconstructed by biome(s) and $\delta^{13}C$ inverse modelling are represented by a grey scale color for the probability distribution and its modal curve (in blue). They are bracketed (in green) by the domain that encompasses both potential climatic niches of both most likely biomes. Modified from Hatté et al. (2008).

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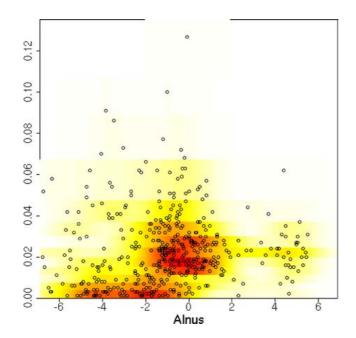


Fig. 6. Alnus distribution: the points are the modern sites, the x-axis is the Aitchison (1982) transform of pollen percents = $\log(P_{\rm alnus}/P_{\rm GrSh})$ (P for percent), the y-axis is the simulated *Alnus* using LPJ-GUESS (in kg carbon m⁻² yr⁻¹) from CRUTS-1.2. New et al. (2000) climate interpolated at each site; the color scale represents the surface fitted to the density of sites (red meaning maximum density).

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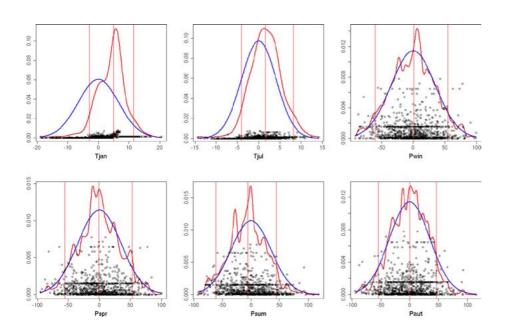


Fig. 7. Prior (blue lines) and posterior (red lines) univariate distributions of the 6 climate variable weighted with the particle importance and smoothed: monthly January and July temperature (in °C of anomaly), seasonal winter, spring, summer and autumn total precipitation (in % of anomaly).

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