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Holocene Vegetation Dynamics and First Land-Cover Estimates in the Auvergne Mountains (Massif Central, France): Key Tools to Landscape Management

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ABSTRACT

A multi-proxy palaeoecological investigation has been undertaken at high spatio-temporal resolution in the Lower Auvergne Mountains (France). It allows us to investigate the Holocene trajectories of landscape evolution arising from the interplay between human impact and adaptability, climate oscillations and environmental evolution. The mechanistic models for the regional vegetation reconstruction applied here provide the first quantification of land cover changes in this region. The results obtained allow an improved understanding of past vegetation dynamics and a discussion of: (1) the natural variability of the vegetation to climate oscillations; (2) the development of the cultural landscape and the land uses involved; (3) the timing and the extent of the landscape openness; and (4) the richness in vegetation units within the landscape mosaic measured by the floristic diversity. These long-term changes highlight the sensitivity of these mountainous landscapes: having formed socio-ecosystems that have been shaped over millennia. It is therefore crucial to consider this ecological and cultural heritage when directing future sustainable management plans.

1. Introduction

The nomination of the "Chaîne des Puys" to the UNESCO World Heritage list makes the development of sustainable management strategies of current landscapes of the Auvergne mountains a pressing concern (Ballut *et al*., 2012; Miras *et al*., 2015). The development of such strategies is a priority as human-induced ecological disturbances are already being observed, particularly a loss in biodiversity in different plant communities (Carrère *et al*., 2014). The causes of this are numerous and include the destruction of natural habitats, a widespread enhanced erosion and organic pollution. Although the Chaîne des Puys is located in a Natural Park ("Parc Naturel Régional des Volcans d'Auvergne"), this volcanic mid-mountain area (up to 1465 m asl) is characterized by a relatively dense human occupation. Thus, anthropogenic pressure is current and mainly induced through agropastoralism and tourism. The process of environmental-decision making must therefore ensure environmental quality, biodiversity conservation and restoration of ecosystem services without preventing socio-economic development, which is vital for this rural territory.

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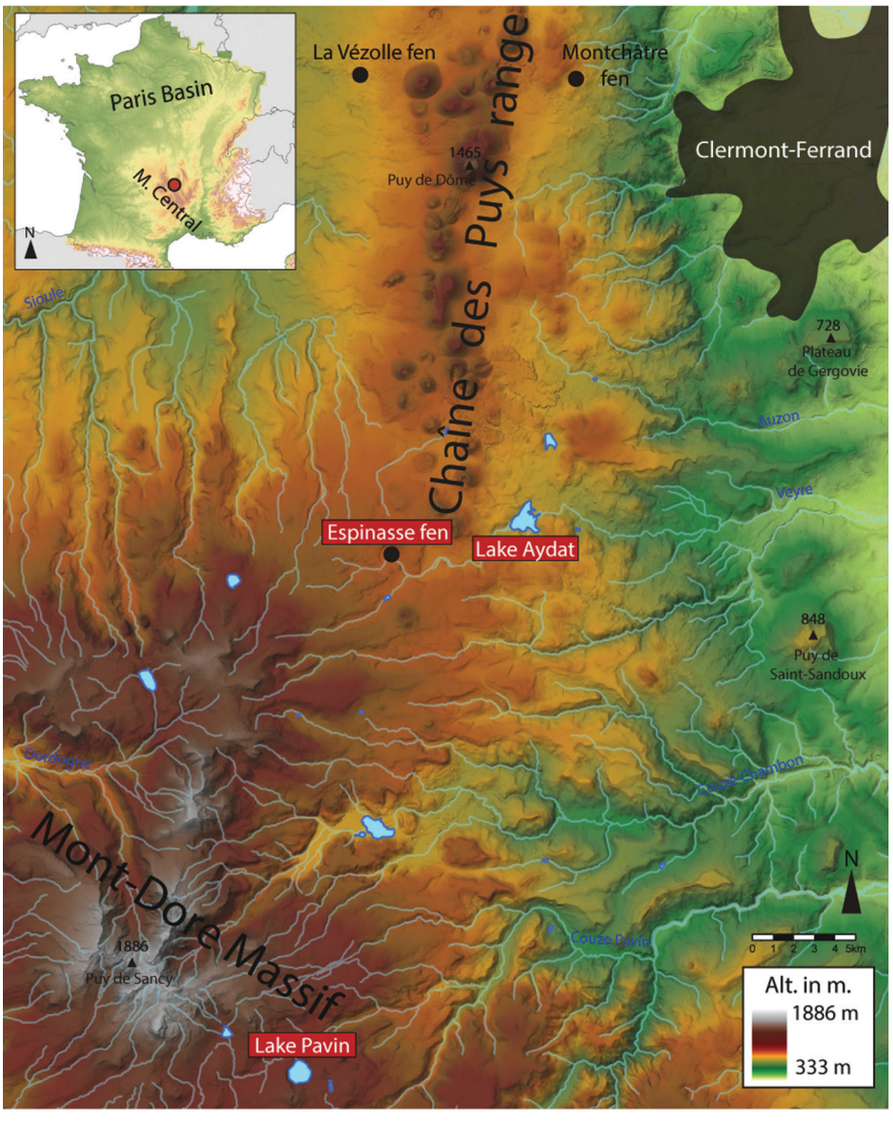


Figure 1. Location of the Lower Auvergne Mountains within France and situation of the palynological sites cited.

Previous research has underlined that several fresh insights for the governance, conservation and promotion of landscapes can be gained from palaeoenvironmental research (*e.g.* Ekblom, Gillson, 2017; Mercuri, 2014; Whitlock *et al*., 2017). In the first place, palaeoenvironmental research provides a long-term perspective on the complex interplay between human impact and adaptability, climate oscillations and environmental evolution. Secondly, it allows the reconstruction of the long-term development of landscapes which are defined nowadays as coupled human-environment systems – named socio-ecosystems – with diverse and complex linkages over time (Turner *et al*., 2003). Finally, it allows a better characterization through time of the ecological processes before, during and after an impact (both natural or human-induced). Moreover, recent advances in palynology play an important role in this issue as follows: (1) the multi-proxy study of numerous high-quality pollen stratigraphical sequences at high spatio-temporal scales (*e.g.* in mountains areas, Ejarque *et al*., 2010; Jouffroy-Bapicot *et al*., 2013); (2) the use of mechanistic models for regional vegetation quantification (*e.g.* Gaillard *et al*., 2010; Mariani *et al*., 2017; Mazier *et al*., 2012); and (3) the use of pollen-assemblage richness indexes which trace the evolution of the floristic diversity (Birks *et al.*, 2016) and which particularly assess the influence of woodland clearance on biodiversity, in the case of a combined study with land-cover estimates.

The overall objective of this paper is to investigate the Holocene vegetation history in the Lower Auvergne Mountains and the long-term shaping of this cultural landscape as inferred by the high-resolution study of three lacustrine and peat sequences. In addition, the first quantitative reconstructions of land cover have been performed in order to examine large-scale changes in land cover. REVEALS converts pollen data collected from large sites or multiple small sites into plant cover estimates at a macro-regional level defined at a spatial scale of c. 100×100 km (Sugita, 2007; Trondman *et al*., 2016). Consequently, the first results obtained are only discussed with regard to the major trends of plant-landscape trajectories at a macro-regional scale. Finally, the potential of the obtained palaeoenvironmental

data for the development of improved landscape management strategies is explored in terms of:

- What were the baseline conditions of the vegetation and what is its natural ability to change with climate variations?
- What is the landscape evolution as analysed both in its temporal and spatial dimensions?
- What are the main potential drivers of landscape change?
- What is the ecological inheritance derived from these cumulative impacts and what can be learned for landscape management?

2. The case studies

This study focuses on three sites (2 lakes and 1 fen) within the Auvergne region. Two sites near to each other are located at the south of the Chaîne des Puys (Figure 1): Lake Aydat (N 45°39.809′; E 2°59.106′; surface area: 0.61 km^2, 837 m asl), which originated from the damming of the Veyre River by a basaltic flow at c. 8551±400 cal. BP (Boivin *et al*., 2004); and Espinasse fen (N 45°38'; E 2º53; surface area: 0.21 km^2; 1160 m asl), which occupies a basaltic maar, formed around 12,400 cal. BP (Camus, 1975). Lake Pavin (N 45°39.809′; E 2°59.106′; surface area: 0.44 km^2; 1197 m asl) is a maar lake located in the Mont-Dore area. It originates from a phreato-magmatic explosion occurring c. 7000 years ago (Juvigné *et al*., 1996). Age-depth models and other details and references are presented respectively in Lavrieux *et al*., 2013, Miras *et al*., 2004, and Chassiot *et al*., 2018. Lakes Pavin and Aydat, and Espinasse fen pollen sequences cover approximately the last 7000, 6730 and 5500 years respectively. Different mass wasting deposits have been evidenced in the lacustrine sequences and prevent the performing of pollen analysis, between: (1) c. 3180±90 and 1770±60 cal BP in Lake Aydat; and (2) c. 1470±160 and 660±30 cal BP in Lake Pavin (Lavrieux *et al*., 2013; Chassiot *et al*., 2016, respectively).

The study area corresponding to the Lower Auvergne Mountains lies in the mountain vegetation belt mainly characterised by acidophilous and neutrophilous beech forests (essentially *Asperulo–Fagion*, *Fageto–Scilletum lilio-hyacinthi* communities) interspersed with fir (*Abies alba* Mill.), and secondarily by calcicole beech woodlands (*Cephalanthero-Fagion* communities) (Freydier Dubreuil, 2004). Today, the landscape is patchy and heterogeneous, dominated by grazed grasslands, meadows, heathlands and extensive areas of reforestation (mainly non-native coniferous trees, such as *Picea abies* L. or *Pseudotsuga menziesii* Mirb.).

3. Material and methods

Samples for pollen analysis were prepared using standard procedures (Faegri, Iversen, 1989). Pollen data were calculated as the percentage of total pollen excluding Cyperaceae, aquatic plants and fern spores. More methodological details are available in Miras *et al*., 2004; 2015 and Chassiot *et al*., 2018. As the complete pollen diagrams were previously published in the above-mentioned studies, we present here synthetic pollen diagrams showing key taxa for the vegetation reconstruction. Summary curves adopt an "indicator species" approach (*sensu* Behre, 1981), summing pollen taxa relative to their ecological affinity (Antonetti *et al*., 2006) and to their indicative value of anthropogenic impact (Guenet, 1986) in Auvergne. As the main objective of our palaeoenvironmental reconstruction is to track the main trends in "forested *vs* open landscape" and "natural *vs* anthropogenic landscape" through time, 9 summary curves have been plotted:

- The "Riparian Vegetation" curve which represents the percentage values of *Alnus*.
- The "Heliophilous Trees" curve which sums the percentage values of *Betula*, *Corylus* and *Pinus.*
- The "Diversified Oak Woodland" curve which groups the percentage values of the following pollen types: deciduous *Quercus*, *Tilia*, *Fraxinus* and *Ulmus.*
- The "Mountain Woodland" curve which combines the percentage values of *Fagus* and *Abies* pollen.
- The "Grassland" curve which corresponds to the Poaceae pollen values.
- The "Crop" curve which gathers together the pollen indicators of cultivated plants such as Cerealia-pollen type and *Secale*-type.
- The "Disturbance-related plants" curve associates the percentage values of *Plantago*-type (combining undifferentiated *Plantago*-type, *Plantago lanceolata*-type and *Plantago major/media*-type) and *Artemisia*. These two pollen types are recognised as strong indicators of regional human-induced environmental disturbance (*e.g.* grazing) in mountain areas (Court-Picon *et al*., 2006; Ejarque *et al*., 2011).
- The "Heathland" curve combines the percentages of Ericaceae and *Calluna* pollen-types.
- The "Wetland" curve which corresponds to the Cyperaceae pollen values.

Results obtained on these three high-quality pollen sequences allow us to perform the first quantitative vegetation reconstruction (*sensu* Sugita, 2007) in this region. As the relationship between pollen percentages and vegetation cover is non-linear (*e.g.* Faegri, Iversen, 1989), empirical-based modelling taking into account differential pollen productivity and dispersal capabilities of plant taxa are necessary to estimate past vegetation cover from sedimentary pollen assemblages (Gaillard *et al*., 2010). The Landscape Reconstruction Algorithm (LRA), proposed by Sugita (2007), and which employs the REVEALS model, aims to obtain estimates of vegetation abundance on a macro-regional scale (c. 100×100 km). This model benefits from including both Pollen Productivity Estimates (PPEs), to adjust for differential pollen productivity, and dispersal and deposition models for atmospheric particles, to correct for

Table 1. PPEs (with their standard errors) and fallspeed of 18 pollen taxa according to Mazier *et al.* (2012).

Taxon	Fallspeed	PPEs	PPE.errors
Abies (fir)	0.12	6.88	1.44
Alnus (alder)	0.021	9.07	0.1
Artemisia (common mugwort)	0.025	3.48	0.2
Betula (birch)	0.024	3.09	0.27
Calluna (common heather)	0.038	0.82	0.02
Cereal*	0.06	1.85	0.38
Corylus (hazelnut)	0.025	1.99	0.2
Cyperaceae	0.035	0.87	0.06
Ericaceae	0.038	0.07	0.04
Fagus (beech)	0.057	2.35	0.11
Fraxinus (ash)	0.022	1.03	0.11
Plantago (plantain)*	0.028	1.086	0.162
Pinus (pine)	0.031	6.38	0.45
Poaceae (grassland)	0.035	1.0	0.0
Quercus (oak)	0.035	5.83	0.15
Secale (rye)*	0.06	3.0	0.374
Tilia (lime)	0.032	0.8	0.03
Ulmus (elm)	0.032	1.27	0.05

*PPEs for these taxa were re-calculated from existing values published in Mazier *et al.* (2012) to combine taxa with variable productivity estimates using variance-weighted mean. *Plantago* is a sum of *P. media*, *P. montana* and *P. lanceolata*. Cereals are a combination of Cerealia and *Secale* pollen types.

the differential dispersal of pollen types. To account for pollen dispersal differences in our case studies, REVEALS was run using the widely deployed Gaussian Plume Model (GPM) (Prentice, 1985; Sugita, 1994). The GPM is based on Sutton's air pollutant plume dispersion equation (Sutton, 1953), which was calibrated using the concentration of particles (*e.g.* pollen) several hundred metres downwind from a point source as spreading outward from the centreline of the plume following a normal probability distribution. REVEALS requires large sites (ideally >1 km^2) (Sugita, 2007) or multiple small-sites (Trondman *et al*., 2015); we thus ran the model on the combined Aydat, Espinasse and Pavin datasets in order to reconstruct the macro-regional vegetation cover changes. This reconstruction is based on the same vegetation groups as those presented before and for which pollen productivity estimates (PPEs) of pollen taxa were available. PPEs and pollen fall speeds for the chosen taxa were derived from the work of Mazier *et al.* (2012), who derived datasets of average PPEs for major European plant taxa (Table 1). We selected PPEs from the Standard 2 dataset of Mazier *et al.* (2012), which minimises the effect of outliers in the PPEs calculation from different locations and was deemed to be the most objective dataset in order to obtain robust vegetation cover estimates in NW Europe (Mazier *et al*., 2012; Trondman *et al*., 2015). The REVEALS model was run for single sites using the DISQOVER package (Theuerkauf *et al*., 2016) for R employing the Gaussian Plume Model with a wind speed set to default (3 $m \cdot s^{-1}$). The compilation of three sites was run using the R script available at https://github.com/petrkunes/LRA.

Rarefaction analysis was undertaken for the 3 case studies in order to assess temporal changes in pollen-assemblage richness or expected number of terrestrial pollen taxa ($E(T_n)$), which is the number of pollen types in a pollen sample at a specific counting sum (Berglund *et al*., 2008). The mean pollen sums (hygrophytic plants excluded) are around 500 pollen grains for Pavin and Aydat sequences and around 300 pollen grains for the Espinasse sequence (because of the bad pollen preservation). The rarefaction analysis of the pollen data used a base pollen sum of 106, 213 and 417 for the Espinasse, Pavin and Aydat sequences, respectively. The pollen-assemblage richness can be interpreted as an approximate measure of the floristic richness of the vegetation in the pollen source area and of the degree of mosaic configuration of the landscape (Birks *et al*., 2016).

4. Results

4.1 Temporal trends in pollen-assemblage richness at a regional scale

The pollen-assemblage richness indexes (expected numbers of taxa $E(T_n)$) obtained in the 3 study sites are presented in Table 2. Taken together, all these results underline different temporal trends in palynological richness for the Lower Auvergne Mountains since the mid-Holocene (Figure 2). The first time-period (P-1, A-1 and E-1), between c. 6900 and 5700 cal BP, is mainly characterized by an increasing

Table 2. Evolution through time of the expected number of terrestrial pollen taxa (E(Tn)) for the 3 study sites.

Sequence	Zone	Depth (cm)	Estimated Age (cal. BP)	$E(T_n)$	Comments
PAVIN	P-6	164 to 1	475 to sub-present	29.53 to 28.91	oscillating values within a decreasing trend, especially between 120 and 87 cm (ca. 278 and 180 BP)
	P-5	202 to 174	644 to 507	20 to 36.48	increasing trend
	P-4	656 to 644	1750 to 1630	18.12 to 15.58	overall stability
	P-3	781 to 667	3020 to 1860	16.74 to 22.52	increasing trend with values up to 20 since 731 cm (2460 BP)
	P-2	968 to 830	5820 to 3690	17.16 to 19.35	oscillating values at low levels; punctual increases at 913–898 cm (4900–4700 BP), at 862–830 cm (4150–3700 BP), at 25 cm (sub-present)
	P-1	1044 to 973	6880 to 5900	17.63 to 21.07	overall stability of the values; slight increase at the end of the zone
AYDAT	A-11	69 to 1	70 to sub-present	50.47 to 46.96	decreasing trend
	A-10	139 to 85	203 to 99	46.91 to 55.16	increasing trend, up to maximal values
	A-9	198 to 149	316 to 222	46.99 to 40.96	slight decreasing trend
	A-8	536 to 225	963 to 368	51.83 to 49.25	overall stability of the values at a high level
	A-7	717 to 559	1482 to 1007	46.33 to 48.40	noticeable increasing trend
	A-6	775 to 728	1769 to 1537	31.54 to 26.49	overall stability at substantial levels
	A-5	835 to 777	3406 to 3186	26.04 to 23.76	decreasing trend
	A-4	962 to 853	3904 to 3475	24.92 to 36.65	noticeable increasing trend
	A-3	1160 to 978	4725 to 3968	26.25 to 22.55	overall decreasing trend except a maximum value (up to 40.55) at 1047 cm (4250 BP)
	A-2	1404 to 1176	5812 to 4794	20.01 to 33.91	oscillating values at lower levels than the previous zone; values increase since 1216 cm (4970 BP)
	A-1	1596 to 1429	6727 to 5929	26.34 to 31.70	slight increasing trend
ESPINASSE	E-10	54 to 14	350 to 119	25 to 13.62	overall decreasing trend down to minimal values
	E-9	109 to 59	667 to 379	23.35 to 18.52	significant decreasing trend
	E-8	169–119	1209 to 724	19.13 to 25.11	after a drastic decrease, values increase up to a first maximum (25.10) at ca 724 BP
	E-7	349 to 199	2820 to 1503	16.15 to 24.19	gradual increasing trend with punctual increases at 349 cm (2800 BP), 289 cm (2300 BP), 269 cm (2150 BP) and 219 cm (1700 BP)
	E-6	629 to 359	4444 to 2904	13.79 to 11.32	decreasing trend with slight punctual increases at 560 cm (4100 BP), and 519 cm (3900 BP)
	E-5	769 to 639	4900 to 4493	17.27 to 18.86	slight increasing trend between moderate values
	E-4	829 to 779	5087 to 4932	20.21 to 15.54	decreasing trend
	E-3	969 to 839	5523 to 5118	15.99 to 20.72	increasing trend
	E-2	1019 to 979	5679 to 5555	19.99 to 15.31	slight decreasing trend
	E-1	1049 to 1029	5773 to 5710	17.9 to 21.69	slight increasing trend

trend of $E(T_n)$ with maximal values which slightly exceed 30 (A-1). The second time-period (E-2/6, A-2/3, P-2), between c. 5700 and 4000 cal BP, is defined by decreased values in comparison with the previous zone. These values oscillate continuously around 20, with minimal values broadly observed between c. 5700 and 5000 cal BP (A-2, E2 and first part of E-3 and of P-2). Slight increases, which are both different and site-related, are nevertheless underlined within this decreasing trend at c. 5500–5100 cal BP (E-3), c. 5000–4800 cal BP (end of A-2, with maximal values up to 34 at c. 4800 cal BP), c. 4900–4500 cal BP (E-5, P-2), c. 4200/3900 cal BP (A-3, middle of E-6, end of P-2). Between c. 3900 and 2000 cal BP (A-4/5, E-6/7, P-2/3), the evolution of $E(T_n)$ follows once more an oscillatory

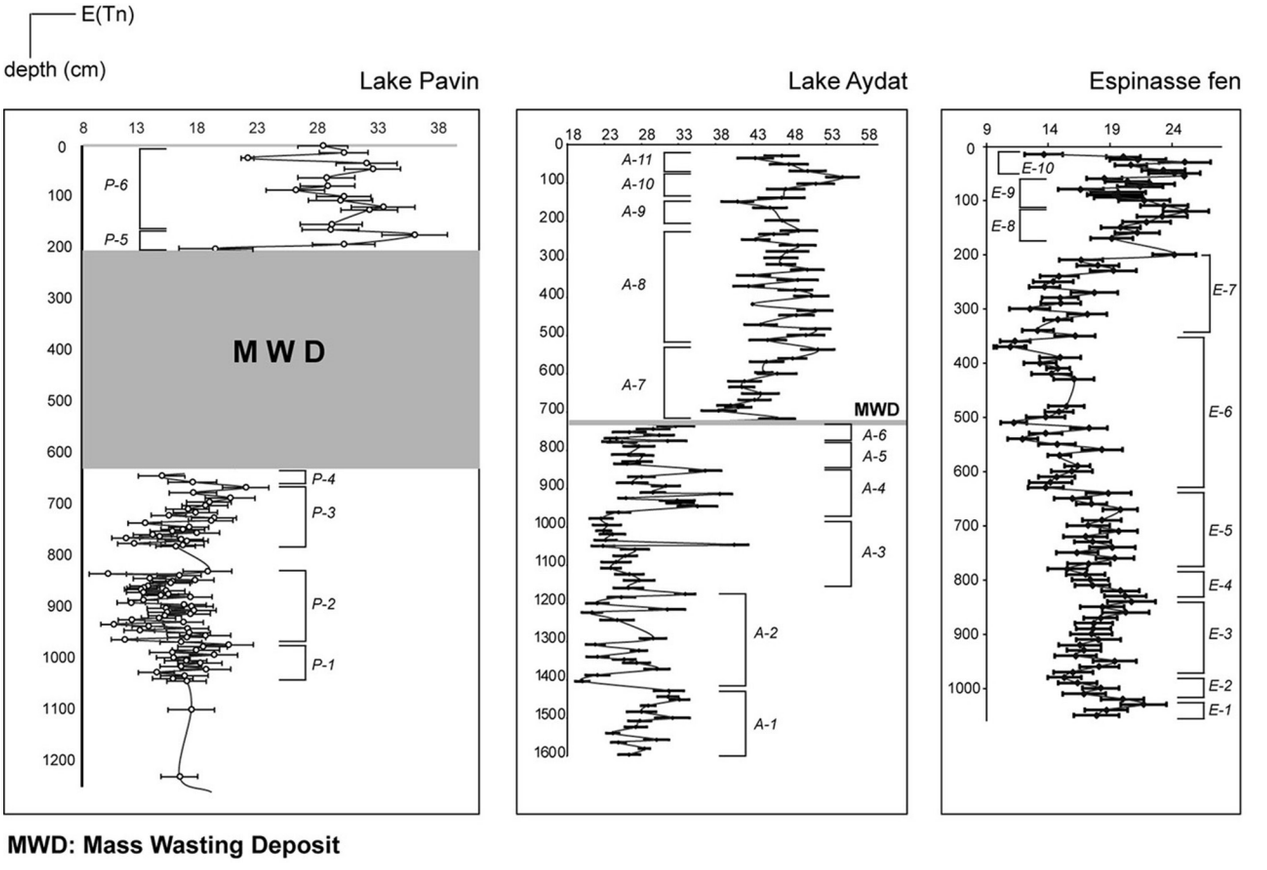


Figure 2. Pollen assemblage richness indexes [Expected number of pollen taxa E(T_n)] based on rarefaction analysis of pollen data from Lakes Pavin and Aydat and Espinasse fen.

pattern, though around higher values than the previous zone. Remarkable increases of E(T_n) are observed between c. 3900–3500 cal BP (A-4, end of P-2). Subsequently, values follow a gradual increasing trend between c. 3800 and 1500 cal BP (P-3/4, E-7, A-6), with an increased tendency especially between 2000 to 1500 cal BP. The following time-period is mainly marked by a progressive and substantial rise of E(T_n) from 1500 cal BP to recent times (E-8/10, A-7/10, P-3/6). Maximum values are reached in the 3 study sites just posterior to 900–600 cal BP in particular. Only 3 different site-related breaks in this tendency were revealed: between c. 670–380 cal BP (E-9) and between 310–120 cal BP (A-9, E-10, the first half of P-6, with an overlapping of the decreased values from the 3 sequences between c. 310 and 220 cal BP). Finally, the last time-period (A-11, end of P-6) is characterized by a substantial decreasing trend of E(T_n), especially since c. 70 cal BP until the sub-recent period.

4.2 Comparison between pollen percentages and first quantitative reconstructions

Figure 3 summarizes the pollen percentages obtained separately on the 3 study sites and, on the combined Aydat, Espinasse and Pavin datasets and REVEALS estimates for forest and non-forest taxa. These data allow us to characterize the regional vegetation cover of the Auvergne Mountains since c. 7000 cal BP. Pollen percentages of the tree taxa display mean values oscillating between 80% and 90% between approximately 7000 and 2000 cal BP. This high amount of tree pollen indicates that the landscape was largely dominated by forests, both at local and regional scales, during this earliest time-period. Nevertheless, the decreasing trend of the oak woodland values (from 50 to 25% approximately) is coeval with an increasing trend of the frequencies of the mountain woodland (from 5 to 55% approximately) between c. 6650 and 5250 cal BP. This suggests a large-scale woodland shift. Our land-cover estimates confirm the macro-regional extension of the diversified oak woodlands, which account for about 65% between c. 7000 and 6650 cal BP. These estimates also highlight the noticeable over-representation of this vegetation group in the pollen percentages and the under-representation of the mountain woodlands which cover c. 75% of the macro-regional landscape since c. 5600–5500 cal BP. During this period, pollen percentages of grassland progress (from c. 3% to 15%) as well as those of wetland (c. 1 to 10%). Percentages values of heliophilous trees present a decreasing trend but remains at substantial rates (from 35 to 15%). Quantitative reconstruction shows a slight over-representation of the heliophilous trees and a noticeable under-representation of the herbaceous taxa

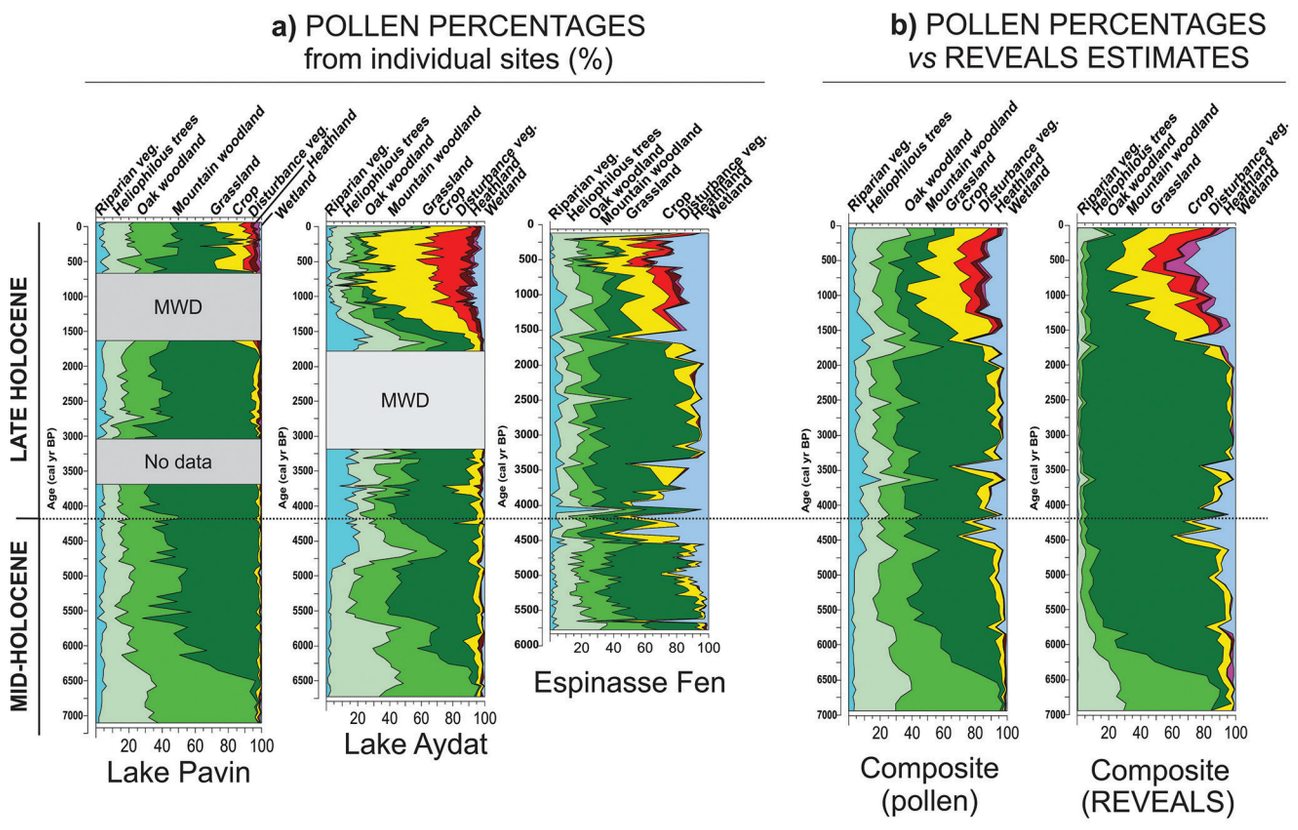


Figure 3. (a) Synthetic percentage pollen diagrams of Lakes Pavin and Aydat and Espinasse fen (MWD: Mass Wasting Deposit). (b) Comparison between synthetic percentage pollen diagram of the combine dataset and vegetation cover percentages.

and heathlands in the pollen percentages. Herbaceous and tree heliophilous taxa and heathlands account for 35% of the macro-regional land cover at the beginning of the 7th millennium and for 25% one thousand years later. During this period, it is noteworthy that herbs and heathlands gradually replace trees as the dominant heliophilous plant component in the macro-regional landscape.

During five millennia of absolute domination of forests on the regional landscapes, different phases of woodland openings have been previously interpreted as phases of human impact (Chassiot *et al*., 2018; Miras *et al*., 2004; 2015): (1) in Lake Aydat: c. 6000–5750, c. 4900–4600, c. 4100–4000, and c. 3900–3500 cal BP; (2) in Espinasse fen: c. 5750–5650, c. 5500–5400, 4550–4450, 4150–3900, and c. 3300–2200 cal BP; and (3) in Lake Pavin: c. 5000–4600, 4100–3850, 3000–2550, and 2400–2050 cal BP. According to the land-cover estimates, these forest regressions are limited as woodland-dominance persists, covering 70–80% of the macro-regional landscape. Moreover, recovery of both tree pollen percentages (up to 90%) and quantitative reconstructions (up to 70%) are recorded just after these episodes of clearance. Nevertheless, higher values of grasslands (up to 10% both in percentages and in quantitative reconstructions), a noticeable record of heathlands and disturbance-related plants, more regular presence of crops and the slight revival of the heliophilous trees (around 10% in percentages and less than 5% in quantitative data) suggest a tendency to less dense forests and/or a trend to a patchier regional landscape between c. 3000 and 2000 cal BP.

The main feature of the pollen results for the period between c. 2000 and 250 cal BP is the gradual decline in the tree pollen percentages (from 95 to 50%). REVEALS estimates obtained for the same period reveal that macro-regional forest cover declined from 95 to 30%. Our land-cover estimates suggest a significant under-representation in the pollen percentages of the proportion of open and human-induced vegetation. It is noteworthy that crops, which account for a negligible presence until c. 1500 cal BP, rise to 20% of the macro-regional land-cover firstly around 800 cal BP, and especially after 500 cal BP (when percentages oscillate between less than 5% to 15%). This gradual decline in forest cover is associated with an expansion of grasslands and heathlands, which gradually compose an open patchy regional landscape. Some slight renewals of tree pollen representations are observed both in percentages and in REVEALS estimates between c. 1100/1000 cal BP, 875/750 cal BP and 500/375 cal BP (respective percentage values: 50, 60 and 55%; respective land cover estimates: 50, 40 and 30%). Percentage values and REVEALS cover estimates of grasslands, crops and other anthropogenic pollen indicators remain at a high level during these periods.

Wetlands also progress and the comparison between their percentages and the REVEALS estimates underline their slight under-representation throughout the 7 millennia. In this sense, two phases of noticeable expansion of wetlands are evidenced both in pollen percentages and in REVEALS estimates: (1) c. 5000–3500 cal BP (from 10 to 30% in pollen percentages and from 15 to 35% in REVEALS estimates), and (2) c. 1250–250 cal BP (until 20% in percentages and until 30% for land-cover estimates). The comparison between pollen percentages of the riparian vegetation (*Alnus*, from c. 5% to 20%) and its REVEALS estimates (up to c. 5%) indicates a clear over-representation of this vegetation type in the percentage values since the mid-Holocene.

Subsequently to c. 250 cal BP, the last time-period start is mainly defined by a clear and progressive revival of the tree pollen amount which explains its substantial increases in percentages (up to 70%) and the REVEALS estimates (up to 45%). Heliophilous and pioneer trees, as well as mountain woodlands, are particularly affected by this large re-expansion of forests. A noticeable decreasing trend is discernible in the pollen values of herbaceous and human-related plants.

5. Discussion

5.1 Mid-Holocene baseline conditions and first human impacts

Palynological data allow us to characterize the natural variability of the vegetation of the Lower Auvergne Mountains under natural drivers (especially climatic fluctuations), prevailing during the mid-Holocene. These "reference" conditions for the vegetation landscape that existed in the absence of extensive human impacts mainly consists of a truly forested landscape developed both at local, regional and macro-regional scales as early as c. 7000–5500 cal BP. This pattern of woodland dominance, prevailing during this period, does not imply that the landscape remained unchanged. Indeed, a progressive substitution of the diversified oak woodlands by the mountain forests composed of beech and fir is evidenced between c. 6650 and 5250 cal BP. This gradual replacement is particularly significant from c. 5600–5500 cal BP, when these dense mountain woodlands began their maximum extension. This large-scale woodland change is likely related to the wetter and cooler climate conditions in the mid-Holocene (Magny, Haas, 2004). During this gradual vegetation shift (c. 6650–5250 cal BP), a more heterogeneous vegetation landscape developed and open herbaceous areas appeared. In the region, human activities are evidenced by palynological data throughout this period (Vézolle fen: Michelin *et al*., 2001; Espinasse fen: Miras *et al*., 2004; 2015, Figure 1), suggesting that this more fragmented forested landscape may have been attractive for Middle Neolithic people, who may have consequently strengthened the degree of fragmentation of the landscape.

5.2 The long-term development of the cultural landscape

Palynological data suggest that the vegetation was continuously impacted by human activities, with some temporal thresholds evident from as early as the late Neolithic (c. 4900–4400 cal BP) or the Early Bronze Age (c. 3900–3500 cal BP) – see Figure 4. Human activities induced rapid vegetation changes from dense woodlands towards more open and patchy landscapes. Archaeological data are relatively scarce for the Late Neolithic in the Lower Auvergne. However, the Early Bronze Age (mainly between c. 3850–3450 cal BP) is a key period for the human occupation, especially in the neighbouring Limagne area (*e.g.* Sévin-Allouet, 2010; Thirault, 2013). The palynological and archaeological data thus attest that this phase is a threshold period in the occupation of the Lower Auvergne uplands and lowlands. Nevertheless, these prehistoric human impacts are systematically followed by a renewal of dense forests, which indicates that the climate was the predominant driver of vegetation changes (Figure 4). Despite this persistent regeneration, a slight loss of resilience in the forested landscape dynamics in the Lake Aydat watershed can be inferred by the pollen percentages of tree taxa, which never recover the values reached before the Early Bronze Age impact. In this case, the "pristine" forested landscape may have been converted by more repeated clearances and more intense and permanent agriculture into a "semi-natural", patchy and grass-rich landscape (Miras *et al*., in press). However, the regional dominance of the forest prevails until c. 2000 cal BP in the Lower Auvergne Mountains.

The comparison of the pollen sequences highlights the successive and alternate phases of local human impacts between c. 6500 and 2000 cal BP. At a local and regional scale, these changes draw a complex spatial pattern of landscape shaping (Figure 4), which result in the construction of mosaic-like shifting manipulated landscapes over space and time. Most likely, this relates to the high adaptability of prehistoric societies towards climate variations, resulting in non-linear relationships between human activities and climate. In this sense, the majority of the phases of human impact revealed by the palynological data spanned periods characterized by an oscillating climate (Figure 4). Thus, it appears necessary to analyse both landscape shaping and human adaptability in terms of mobility and/or reorganisation of human activities, both at local and regional scales.

During historical times, especially since c. 2000/1500 cal BP, these uplands were more or less permanently occupied and human impact became the main driver of the vegetation changes towards a patchy open agricultural landscape (Ballut *et al*., 2008; Miras *et al*., 2015). This is especially evident in the pollen diagrams (both in percentages and REVEALS estimates) by observing the curves of open herbaceous areas (mainly grasslands), crops, and disturbance-related plants (Figure 3).

5.3 Timing and extent of the Late Holocene woodland clearances

During historical times, the progressive and widespread transformation of the landscape of the Auvergne uplands can

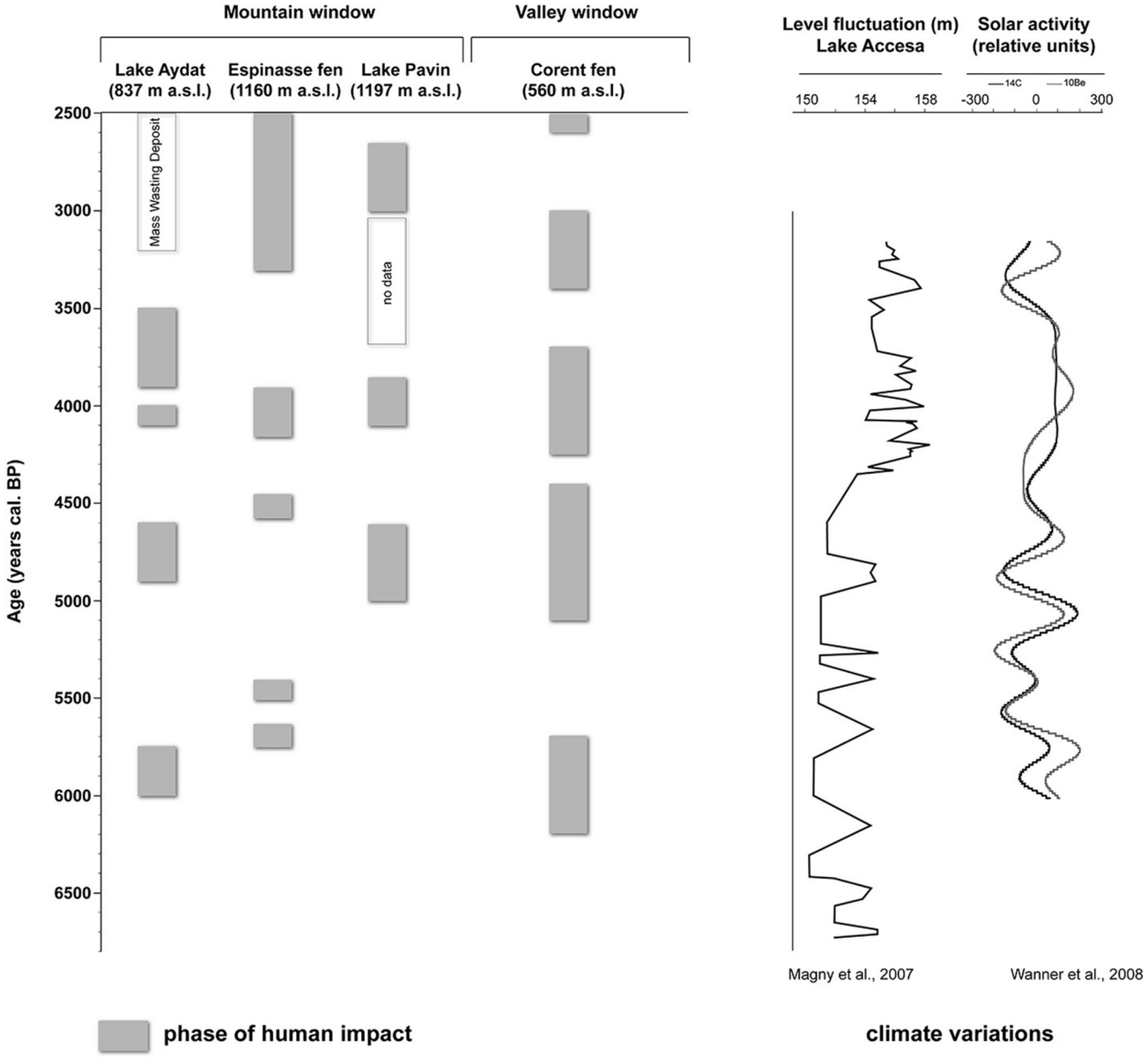


Figure 4. Phases of prehistoric and protohistoric human impact revealed by palynological data (percentage values) in the Lower Auvergne Mountains compared to climatic oscillations (modified after Miras *et al.*, in press).

be divided into two steps. The first comprises a progressive substitution of a prehistoric wooded landscape into a grass-rich and fragmented landscape (named Cultural Landscape Form-1). This vegetation landscape is induced by different waves of deforestation initiated from c. 2000/1500 cal BP, and related to agro-pastoral extension (Montchâtre fen: Ballut *et al*., 2008; Miras *et al*., 2004; 2015, Figure 1). At a macro-regional level, the landscape appears to be mixed – forests and open herbaceous areas both sharing 50% of the macro-regional land cover – from c. 1500/1400 cal BP. The second step starting between c. 1000/600 cal BP corresponds to the gradual replacement of the Cultural Landscape Form-1 by a more open and grassland-dominated landscape (named Cultural Landscape Form-2). This form is related to successive deforestations, particularly during the High Middle Ages (c. 9th/12th centuries), Late Middle Ages (c. 13th/15th centuries), and Modern Times (second half of the 17th and 18th centuries). A regional land-cover configuration constituted by 80% of open herbaceous areas and 20% of forests – which is close to the present-day configuration (IFN 2010) – is evidenced as soon as c. 1000/950 cal BP. This is even more evident from c. 700/600 cal BP. This landscape trajectory is a result of socio-economic strategies and land-use practices developed through time and mainly based on crop planting (especially in rye) and grazing activities, which particularly extended from the 16th and the 17th/18th centuries (including the top of the volcanoes for grazing purposes). This expansion of agro-pastoral activities is mainly explained

by the re-organisation of the agricultural religious domains previously created (Ballut *et al*., 2012), some of them as early as the 12th/13th centuries (Miras *et al*., 2004). This period of diverse and extended land uses corresponds to a phase of high floristic diversity. This illustrates that anthropogenic pressure may promote increased vegetational diversity (van Beek *et al*., 2018), at least up to a certain intensity and degree of land use diversity. Subsequent decreases in floristic diversity (between c. 300 and 200 cal BP) may be the manifestation of a new landscape evolution characterized by increased homogeneity of the open landscape structure due to a tendency of land use specialisation in grazing rather than its diversification. This is especially the case during the 17th and the 18th centuries with the creation of large secular husbandry domains (Michelin, 1995). Since the 19th/20th centuries boundary, a further reduction of the floristic diversity indicates that a new land use system (modern agriculture and forestry) overcame an intermediate level of disturbance, which is often associated with a high biodiversity (Berglund *et al*., 2008), and this reduction had a negative effect. Similar results have been evidenced in Northwestern France (van Beek *et al*., 2018).

It is noteworthy that since historical times the development of an open patchy cultural landscape appears to be irreversible whatever the climatic (*e.g.* Little Ice Age) or anthropogenic context (*e.g.* Little Ice Age, war, plague). Only slight renewals of the forest cover are observed at a macro-regional scale around c. 1100/1000, 875/750 and 500/375 cal BP. Despite the renewal, anthropogenic pressure remains at a high level in every case. The first real reversal of this landscape evolution characterized by a strong revival of the forest cover started particularly from around 150 cal BP, at the end of the 19th century, and has progressed particularly after the Second World War. This relates to major socio-economic upheavals mainly characterized by a progressive disappearance of farming activity, a declining grazing pressure and a land use re-orientation towards reforestation, and all this accompanied by a major population exodus of the Auvergne Mountains (Ballut *et al*., 2012).

6. Conclusion: an overview about the ecological legacies

Without wishing to downplay the role of the sub-recent and present-day land uses in the current landscape dynamics, the palaeoenvironmental research performed in the Auvergne Mountains has shown that the current landscape is also the composite result of an ancient and complex socio-environmental history. The long-term accumulation of natural/anthropogenic impacts evidenced and the diverse range of activities developed through time at diverse spatial scales generated ecological legacies, which contribute to determining the current structure of these complex socio-ecosystems and their future trajectories.

This "*memory of the system with regards to past events*" (Moorhead *et al*., 1999, p. 1009) must be now considered in the design of sustainable landscape management and conservation. In this sense, this research underlined and/or addressed:

- the rapidity of plant migration with climate fluctuation and the speed of ecosystem responses to early anthropogenic disturbances, as early as the Middle Neolithic. For instance, during the mid-Holocene, the shift that occurred in forest vegetation took place under climatic controls over about one millennium. This emphasizes the high sensitivity of these ecosystems which must now be considered in the current context of global changes;
- the long-term development of a full cultural landscape from a dense forested Prehistoric landscape to a patchy open agricultural landscape during historical times in all their temporal and spatial dimensions. The model of landscape evolution obtained specifies:
  - the key-periods of appearance/development/disappearance of different vegetation landscapes. The early genesis of a semi-natural regional landscape as early as the Early Bronze Age and its gradual but irreversible shaping into a fragmented, open and agricultural landscape during historical times are important results for modelling landscape trajectories – both at local and regional scales. It is noteworthy that macro-regional scales are also concerned, as similar patterns have been evidenced for periods similar to the above in other Western Mountains (*e.g.* Pyrenees: Ejarque *et al*., 2010) or Mediterranean areas (*e.g.* Po plain, Cremaschi *et al*., 2016);
  - the regional and macro-regional extent of vegetation landscapes, even if further analyses are required (especially in order to obtain new high-quality pollen stratigraphical sequences and PPEs originating from the Auvergne region);
  - the timing of the phases of increased floristic biodiversity and landscape patches or, by contrast, the phases of homogeneous landscape and decreased biodiversity and the responsible triggers (especially the nature and intensity of human activities during the Late Holocene). The characterisation of past reference states (for example the period between c. 900 and 600 cal BP) provide fresh insights (intensity and degree of land use diversity and openness) into the protection and promotion of present-day biodiversity;
  - the drivers involved (natural, anthropogenic and a combination of both). In this sense, the period between c. 2000 and 1500 cal BP represents a tipping point whereby human activities become the sole driver of the vegetation changes;
  - the adaptability of human societies based on the mobility and the complementarity of a diverse range of practices.
- the diachronic cumulative impact on ecological processes concerning ecosystem functioning (*e.g.* the potentially first period of past loss in resilience after

the Early Bronze Age impacts) or dealing with plant biodiversity evolution. In this sense, palynological data allow us to better understand the remarkable sub-recent decline of floristic and landscape diversity. This impact starts early – and subsequently to c. 250 cal BP – and becomes gradually stronger from c. 150 cal BP. This may have deeply affected the system resilience and in consequence its vulnerability to further changes (van Beek *et al*., 2018).

Finally, these palaeoenvironmental data stress both the cultural and historical values of these landscapes as well as their biological value. These mountain landscapes must definitively be defined as equivalent of clusters of cultural ecosystems. This cultural legacy is undoubtedly an extraordinary lever for the socio-economic development of this region.

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