

Biotic responses to rapid climatic changes during the Late Glacial

High-resolution biostratigraphies and biological processes

Brigitta Ammann, Ueli Eicher, Jakob Schwander, Bern, Uli von Grafenstein, Gif-sur-Yvette, Kateřina Nováková, České Budějovice, Stephen Brooks, London, Jacqueline van Leeuwen, Bern, Lucia Wick, Bern und Basel, Pim van der Knaap, Bern

1 Introduction

Understanding climatic changes in the North Atlantic/European region during the Late Glacial is necessary in any attempt to assess effects of future climatic changes, because they were larger and more rapid than fluctuations measured during the meteorologically recorded period. To assess the Late Glacial (and Holocene) climatic changes, especially changes in summer temperatures, biostratigraphies are interpreted by applying so-called transfer functions, which relate today's presence or absence of taxa (species, genera) to modern environmental variables (e.g. summer temperatures; BIRKS 2003).

A different approach to climate reconstruction was used in the studies summarized here: if, and only if, an independent line of evidence for climatic change is available, then these same relationships between taxa and climate variables can be used to assess the biotic response to a climatic change. Presented here is one example from a set of sites studied on an altitudinal transect in the Swiss Alps covering the beginning and the end of the Younger Dryas (AMMANN 2000; AMMANN et al. 2000; BROOKS 2000; SCHWANDER et al. 2000; WICK 2000).

On this altitudinal transect, two sources were used to estimate climatic change independent of the biostratigraphies: (1) oxygen-isotope ratios in carbonates (at Gerzensee, 603 m asl, and Leysin, 1230 m asl) and – if carbonate sediments were not available for the measurement of oxygen isotopes – (2) the amount of organic matter in the lake sediment (as loss-on-ignition at 550°C, at Regenmoos, 1260 m asl, and Zeneggen, 1510 m asl). At Gerzensee, the oxygen-isotope ratios measured on bulk sediment (i.e. biogenically precipitated carbonates such as tubes around *Chara* sp.) were also checked by measurements on mono-specific ostracod samples (VON GRAFENSTEIN et al. 2000). This showed high correlations between isotope values from bulk sediment and from ostracods, indicating that the record was not distorted by reworked material in the bulk carbonates.

Biotic response is estimated here from two biostratigraphies recording changes in groups of organisms that have very different life cycles: vegetation as recorded in pollen stratigraphy includes annuals, biennials and long-lived species, like trees and shrubs that are usually thought to respond slowly to climatic change. Chironomids (non-biting midges, Diptera/insects) go – at least under favorable conditions – through annual life-cycles and may therefore trace climatic changes with little or no time lag.

Time control is a crucial issue when estimating rates of environmental change from a sediment sequence. But because the period of the late Younger Dryas and its transition into the Holocene coincides with a plateau of constant age in the radiocarbon calibration curves, ¹⁴C-dating does not help (unless a great many samples are dated in order to perform wiggle-matching; e.g. GULLIKSEN et al. 1998). Assuming synchronicity of major climatic shifts, such as the beginning and the end of the Younger Dryas in the northern hemisphere, SCHWANDER et al. (2000) propose the correlation of changes of oxygen-isotopes in the NGRIP (North Greenland Ice core Project) ice-core with changes found at Gerzensee and Leysin, thus enabling the application of the time scale from NGRIP to these two terrestrial sites (i.e. in cal yr BP).

2 Material and methods

To illustrate the conclusions about possible biological processes drawn herein, the findings for the site at Leysin in the western part of the Central Swiss Alps (46°20'49.96"N, 7°01'18.20"E, 1230 m asl) are presented here. Leysin belongs to the sites investigated already by EICHER & SIEGENTHALER (1976) and WELTEN (1982). During those investigations, a clear parallelism between pollen and oxygen-isotope ratios around the Younger Dryas could be shown. On new cores taken in 1992 with a modified Livingstone piston corer, the sampling resolution for stable isotopes and pollen were increased by a factor of about 3, and a chironomid stratigraphy analysis was included. Sampling for isotope and biostratigraphies was performed on the same core at identical levels. The methods used for the analyses of pollen and chironomids are given in WICK (2000) and BROOKS (2000), respectively. The biotic changes across the more than 100 pollen taxa and 30 chironomid taxa are summarised in Figure 1 as the scores on the first axis of a principal component

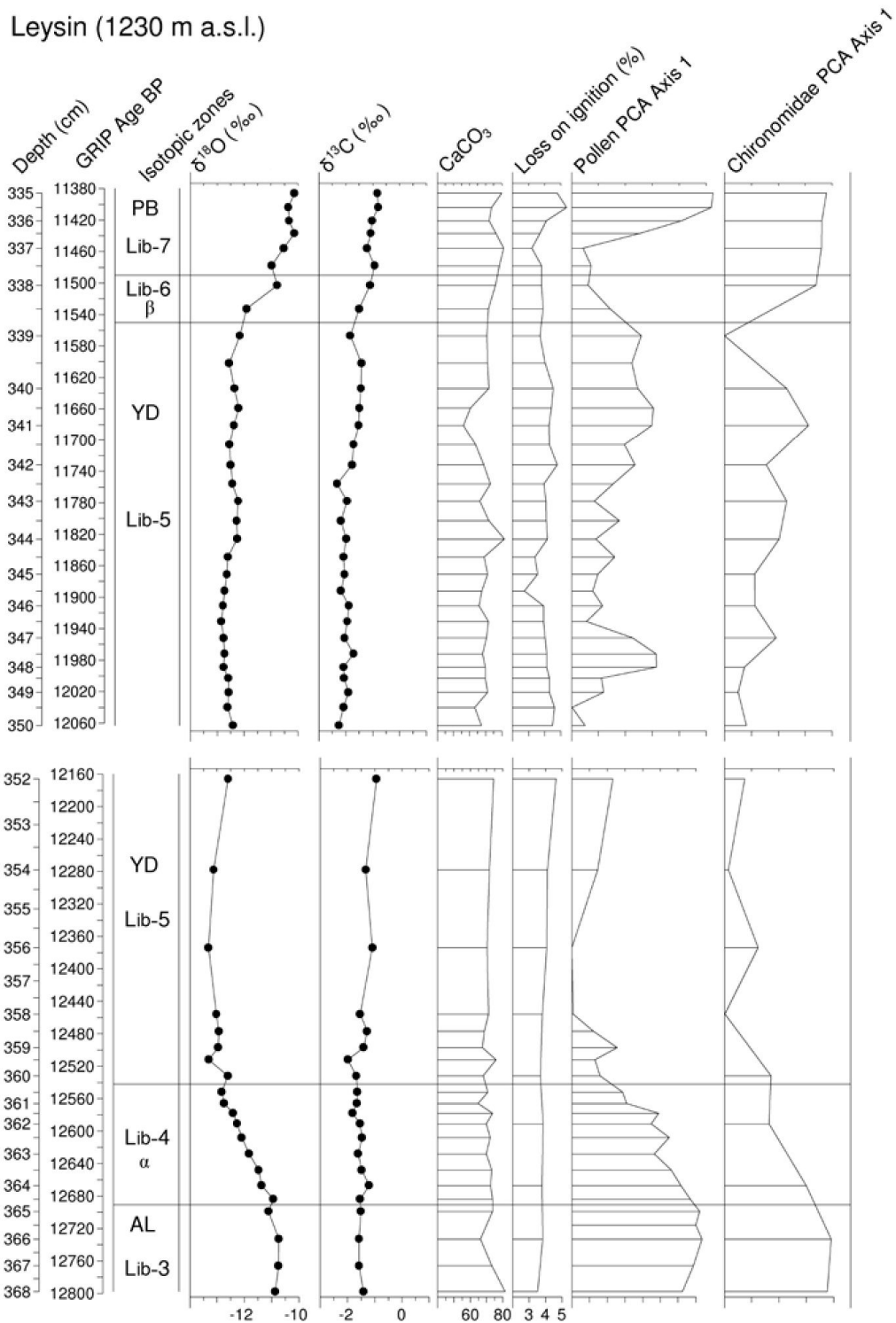


Fig. 1: Transitions at the onset and end of the Younger Dryas at Leysin (1230 m asl) on a linear NGRIP-time-scale (i.e. in cal yr BP)

Isotopic zones Lib stand for «Leysin isotopes on bulk sediments» and show a rapid decline in zone Lib-4 leading into the Younger Dryas (Lib-4), and a rapid increase during zone Lib-6 leading out of the Younger Dryas into the early Holocene (PB for Preboreal, Lib-7). The values on the first PCA-axes for pollen and chironomids summarize the degree of change between adjacent samples for pollen and chironomids.

Le début et la fin du Dryas récent à Leysin (1230 m au-dessus de la mer) sur l'échelle temporelle de NGRIP (i.e. en cal yr BP)
Beginn und Ende der Jüngerer Dryas in Leysin (1230 m ü.M.) auf dem linearen Zeitmassstab von NGRIP (i.e. in cal yr BP)

analysis (PCA). This method was used here because in a preliminary detrended correspondence analysis (DCA) the gradient lengths were smaller than two sigmas (for details see AMMANN et al. 2000). The two time windows of onset and end of Younger Dryas were treated separately (see lower and upper half of Fig. 1). The diagrams have been kept separate because two different cores were used: Leysin core B above 350 cm and Leysin core A below 350 cm. Although their correlation is not certain, the emphasis here was on the two periods of very rapid change.

3 Results and discussion

In Figure 1, the two rapid transitions at the beginning and at the end of the Younger Dryas (YD) are shown by the oxygen-isotope ratios as measured in the bulk sediment (lake marl). The three columns following to the right indicate that contents of $\delta^{13}\text{C}$, carbonates, and organic matter are quite stable across these two transitions; it may therefore be assumed that the changes in $\delta^{18}\text{O}$ are not a result of sedimentary changes but rather of temperature changes (see also VON GRAFENSTEIN et al. 2000). The curves for scores on the first PCA-axes for pollen and chironomid-stratigraphies are parallel during isotopic zone Lib-4 (i.e. the onset of YD). Also, during isotopic zone Lib-6 (i.e. the end of YD), the differences between identical samples are very small (the opposite direction does not mean a seemingly opposite ecology, because it is only a quantitative measure for the overall change between adjacent samples). Thus, it may be concluded that the changes in pollen assemblages do not lag behind the changes in chironomid assemblages, and both do not lag behind the onset of the changes in the oxygen-isotope ratios.

This is more synchronicity than expected. It must therefore be asked which biological processes are responsible for such fast responses to rising summer temperatures as is recorded in the oxygen isotopes. Since the classical discussions about Late Glacial and early Holocene stratigraphies of pollen and beetles in northern England by PENNINGTON (1977) and by COOPE (1977), pollen was often said to be slow to respond to climatic change because of migrational lags. Insects, in contrast, having much shorter life cycles and greater mobility, were thought to trace climatic changes without delay. Here, in contrast, a high synchronicity of responses in plants and insects was found. It is therefore concluded that the biological processes involved in the examples of Windermere in northern England and Leysin are not the same.

Since these early studies, multidisciplinary analyses of biostratigraphies have been made at a number of sites.

The most comprehensive study including the Younger Dryas was probably completed at Kråkenes in western Norway by BIRKS et al. (2000) where, apart from pollen and chironomids, seven other biostratigraphies were analyzed. Because of the lack of carbonates due to the geological setting, the analysis of oxygen isotopes was not possible, but the degree of synchronicity among the biotic changes can be estimated because the biostratigraphies were also developed from a single master core. Besides the climate reconstructions, one of several major findings at Kråkenes was that

«the reaction times to the sharp temperature changes at the start and end of the Younger Dryas were very rapid and occurred within a decade of the temperature change» (BIRKS et al. 2000: 92).

Biotic changes during the early Holocene, in contrast, were more gradual and not synchronous in the different groups of organisms (BIRKS et al. 2000).

In order to estimate the rapidity of the biotic responses, it was necessary to assess the sampling resolution. On the basic assumption of hemispheric synchronicity for the onset and end of the Younger Dryas, the chronology from NGRIP could be transferred to the sites of Leysin and Gerzensee (SCHWANDER et al. 2000). Consequently, the sampling resolution was estimated to be 17-30 years at Leysin, and 8-15 years at Gerzensee for the relevant transitions.

The categories sometimes made among biological processes involved in response to climate change are the following:

- **Migration:** The limits of biogeographical ranges may change during or after climatic shifts, e.g. restriction of thermophilous species to the south during a glacial period (or to the north in the southern hemisphere) or spreading of thermophilous taxa northwards after an ice age or due to current global warming (e.g. PARMESAN 2006; WALTHER et al. 2002).
- **Building up of a population:** When a taxon has arrived in a new area, the population may at first be very small (just a few individuals). The growth of the population may be slow at the beginning, but for some taxa exponential later, depending on the species and a number of environmental conditions. Population growth then usually declines after reaching a level defined by the «carrying capacity» of the system for that species.
- **Productivity:** In contrast to the other two types of process that work on the level of the population, the changes in productivity occur on the level of the individuals. The width of tree rings or pollen productivity are examples. Not included here are variables such as number of offspring or success of reproduction that would reflect more the process of population growth.

The potential velocity or the time periods required for the three types of process differ widely (and are species-specific):

- Migration or biogeographical migration means shifts of the range limits; it is not to be confused with seasonal migrations, as seen with birds or butterflies. Biogeographical migrations are rather slow, depending on species and their life histories; the latter include parameters such as age at first reproduction, dispersal capacities. Long-lived and slowly reproducing groups, such as trees, are expected to be slower than annual and highly mobile species, such as most insects.
- The growth of populations may require intermediate lengths of time. They are generally faster than migrations but slower than productivity changes.
- Changes in productivity may occur rather quickly: tree ring width usually reflects the condition of the current year, and pollen production often reflects the conditions of the previous year (AUTIO & HICKS 2004; VAN DER KNAAP et al. 2001).

If there are no lags to the isotopic change in both the vegetation (as recorded by pollen) and the aquatic invertebrates (here chironomids), the slowest of the three types of response processes can be excluded. This would be migration, or at least latitudinal migration as is usually understood, for example trees migrating back from Southern to Central Europe. Even dominant trees such as pine and birch, which had arrived during the Late Glacial interstadial (Bölling and Alleröd) did not show delays in their responses to the isotope shifts. From the study of plant macro-remains by TOBOLSKI & AMMANN (2000), it appears that during the Younger Dryas trees were probably locally absent from Leysin, but regionally present: their distance for re-immigration from the valley bottom was so short that it could not be evaluated here due to the sampling resolution of about 30 years. This is an example of an altitudinal but not a latitudinal migration.

4 Conclusions

The following four conclusions may be drawn: (1) Terrestrial and aquatic ecosystems may respond rapidly and synchronously because biological processes on several organisational levels are involved. (2) Time needed for response processes decreases in the following order: migration > population-growth > productivity-change of the individual. (3) If no migrational lags (or only migrational lags shorter than the sampling resolution) are involved, the pollen signal in response to climatic changes can be very fast because the rapid mechanism of changing pollen productivity may be involved. And (4) these findings

do not contradict the classical concepts of IVERSEN (1964), who argued that aquatic organisms (including water plants) may be faster than terrestrial plants in responding to climatic changes because their propagules get transported by water fowl (high mobility), and they do not need soil development. The findings here rather build on these concepts and add to their greater refinement.

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Abstract: Biotic responses to rapid climatic changes during the Late Glacial. High-resolution biostratigraphies and biological processes

Organisms can respond to rapid climatic changes in three ways: (1) adaptation (by evolution, affecting physiology and morphology), (2) migration and population dynamics (including biogeographical changes) and (3) extinction (local or global). Here, the focus is on examples of the second type. Organisms, whether algae, trees, or animals, find their ecological niches in a multi-dimensional space of gradients such as temperature (winter, summer, means or extremes), humid-

ity (soil or air), pH, various nutrients, light. Presence or absence of taxa (species, genera, families) can be related to such gradients. With training sets based on current gradients, they can also be related to environmental changes of the past (e.g. summer mean temperatures or pH). The relationships between the occurrence of taxa and environmental variables can also be used to examine the biotic response to changes based on other proxies, for example, changes in temperature inferred from oxygen-isotope ratios in carbonates or from the content in organic matter of lake sediments. The groups of organisms referred to here are plants (pollen), insects (chironomids) and other aquatic invertebrates. The three Late Glacial periods with very high rates of change in temperature estimates are the transition from the Oldest Dryas to the Bölling (from GS-2 to GI-1 in the Late Glacial, ca. 14 670 cal yr BP), and the beginning and the end of the Younger Dryas (ca. 12 600 cal yr BP, 11 500 cal yr BP respectively).

The «classical» hypothesis was that trees (represented in pollen diagrams) respond more slowly to climatic change than invertebrates (aquatic or terrestrial) because of differences in life cycles. But it is shown here that terrestrial (vegetation) and aquatic (invertebrate) ecosystems may respond synchronously. Three major biological processes are involved in the responses to climatic change:

- (1) Migration – can be slow if, for example, a long-living tree migrated back from a southern refugium.
- (2) Build-up of populations – intermediate velocity, for the process needs time depending on the life cycles of the organisms.
- (3) Productivity – can change rapidly, within a year or a few years (e.g. pollen productivity, tree rings).

The first two of these processes occur on the organisational level of populations, the last one on the level of the individual. These processes develop also in various combinations.

Keywords: Abrupt climatic change, biotic response, Late Glacial, population dynamics

Résumé: Réponses biotiques aux changements climatiques rapides pendant le Tardiglaciaire. Biostratigraphies à haute résolution et processus biologiques

Les organismes peuvent répondre aux changements climatiques de trois façons différentes: par adaptation physiologique et morphologique, par migration et dynamique des populations, incluant les changements biogéographiques, et par extinction locale ou globale. Cet article se concentre sur les exemples du second type. Les organismes, que ce soient des algues, des arbres ou des animaux, créent leur niche écologique dans un espace à plusieurs dimensions

défini par la température (d'hiver, d'été, moyennes et extrêmes), l'humidité (du sol, de l'air), le pH, les nutriments, la lumière. La présence ou l'absence des taxons (espèces, genres, familles) peut être reliée à ces gradients physico-chimiques ou environnementaux. Avec des fonctions de transfert basées sur les gradients existants aujourd'hui, il est possible de lier la présence/absence des taxons aux conditions environnementales du passé (ex. température moyenne en été ou pH). Ces variations à travers le temps peuvent aussi être mises en relation avec les réponses biotiques aux changements climatiques d'autres proxies, tels les changements de température reconstruits ici par les isotopes d'oxygène ou les changements de teneur en matière organique des sédiments lacustres. Les groupes d'organismes utilisés ici sont les plantes (pollen), les insectes (chironomides) et d'autres organismes aquatiques. Les trois dernières périodes tardiglaciaires, qui ont démontré des changements très brusques de température, sont étudiées, plus précisément la période de transition entre le Dryas ancien et le Bölling (GS-2 à GI-1, environ 14 670 cal yr BP), et le début et la fin du Dryas récent (environ 12 600 cal yr BP, 11 500 cal yr BP respectivement).

Une hypothèse «classique» suggérait que les arbres (représentés par le pollen) répondaient lentement aux changements climatiques alors que les invertébrés y répondaient rapidement en raison de leur cycle de vie plus rapide. Cependant, les résultats présentés ici démontrent que les écosystèmes terrestre (végétation) et aquatique (invertébrés) peuvent répondre simultanément. Trois processus biologiques expliquent ces réponses aux changements climatiques. Tout d'abord la migration, qui peut être lente si elle s'effectue à partir d'un refuge localisé au sud. Ensuite, le développement de la population, qui s'effectue à une vitesse intermédiaire car le processus est dépendant du cycle de vie des organismes. Enfin, la productivité, qui peut changer rapidement en une ou plusieurs années (ex. productivité du pollen, anneaux des arbres). Les deux premiers processus s'effectuent au niveau de la population alors que le dernier s'effectue au niveau individuel. Ces processus se développent aussi en combinaisons.

Mots-clés: Changements climatiques brusques, réponses biotiques, Tardiglaciaire, dynamique des populations

Zusammenfassung: Biotische Reaktionen auf rasche Klimaänderungen im Spätglazial. Hochaufgelöste Biostratigraphien und biologische Prozesse

Organismen können auf rasche Klimaveränderungen in dreierlei Weise reagieren: (1) Anpassung (durch Evolution, welche Physiologie und Morpho-

logie betrifft), (2) Migration und Populationsdynamik (inklusive biogeographische Verschiebungen) und (3) Aussterben (lokal oder global). Im Folgenden steht die zweite Gruppe von Reaktionen im Mittelpunkt. Alle Organismen – ob Algen, Bäume oder Tiere – finden ihre ökologischen Nischen in einem multi-dimensionalen Raum, dessen Achsen man sich als Gradienten vorstellen kann: Gradienten der Temperatur (Winter-, Sommer- Mittel- oder Extrem-Werte), der Feuchtigkeit (des Bodens oder der Luft), des pH, der Nährstoffe, des Lichts. Vorkommen oder Fehlen von Taxa (Arten oder Gattungen oder Familien) kann von solchen Gradienten gesteuert sein. In sog. *training sets* wird heutiges Vorkommen oder Fehlen der Taxa an den Gradienten der Gegenwart geeicht; mit den daraus abgeleiteten Transfer-Funktionen können, basierend auf Vorkommen oder Fehlen in der Vergangenheit, Umweltfaktoren und deren Veränderungen rekonstruiert werden (z.B. Sommer-Temperaturen oder pH). Dieselben Beziehungen zwischen Taxa und Umwelt-Gradienten können aber auch verwendet werden, um die Reaktion der Taxa auf Umweltveränderungen abzuschätzen, falls diese aus unabhängigen Daten bekannt sind. Hier wird das Verhältnis der Sauerstoff-Isotope aus biogenen Karbonaten als Mass für die Temperaturen verwendet. Als Organismengruppen wurden Pflanzen (Pollen), Insekten (Zuckmücken, Chironomiden) und andere aquatische Wirbellose untersucht. Die drei Phasen des Spätglazials mit extrem rascher Temperaturveränderung sind der Übergang von der Ältesten Dryas in Bölling (von GS-2 zu GI-1 ca. 14 670 cal yr BP) sowie Anfang und Ende der Jüngeren Dryas (ca. 12 600 cal yr BP und 11 500 cal yr BP).

Die «klassische» Hypothese war, dass Bäume (im Pollendiagramm) wesentlich langsamer auf den Klimawandel reagieren als aquatische oder terrestrische Wirbellose, weil ihre Lebenszyklen so stark verschieden sind. Doch es zeigte sich, dass die Indikatoren der terrestrischen Ökosysteme (Pollen der Vegetation) und der aquatischen Ökosysteme (Wirbellose) synchron reagierten. Drei Gruppen biologischer Prozesse können unterschieden werden:

- (1) Migration – kann langsam sein, z.B. wenn eine Baumart nach der Eiszeit aus einem südlichen Refugium zurück wandert.
- (2) Populationsaufbau – ist von mittlerer Geschwindigkeit, welche vom Lebenszyklus der Art abhängt.
- (3) Produktivität des Individuums – kann sich sehr rasch ändern (innerhalb eines Jahres, z.B. Pollenproduktion oder Jahrring-Breite eines Baumes).

Die ersten zwei Prozesse betreffen die Populationen, der dritte die Individuen. Die Prozesse treten auch in Kombinationen auf.

Schlüsselwörter: Rasche Klimaänderungen, biotische Reaktionen, Spätglazial, Populationsdynamik

Prof. (em.) Dr. **Brigitta Ammann**, Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland.

e-mail: Brigitta.Ammann@ips.unibe.ch

Dr. **Ueli Eicher**, Dr. **Jakob Schwander**, Physics Institute, University of Bern, Sidlerstrasse 5, CH-3012 Bern, Switzerland.

e-mail: schwander@climate.unibe.ch

Dr. **Uli von Grafenstein**, Laboratoire des Sciences du Climat et de l'Environnement (LSCE), Centre Nationale de Recherches Scientifiques (CNRS-CEA), Orme des Merisiers, F-91191 Gif-sur-Yvette, France.

e-mail: Ulrich.Von-Grafenstein@cea.fr

Mgr. **Kateřina Nováková**, University of South Bohemia, Department of Botany, Branišovská 31, 370 05 České Budějovice, Czech Republic.

e-mail: kmikolasova@hotmail.com

Stephen Brooks, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

e-mail: S.Brooks@nhm.ac.uk

Jacqueline van Leeuwen, Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland.

e-mail: VanLeeuwen@ips.unibe.ch

Dr. **Lucia Wick**, Institute for Prehistory and Archaeological Science IPAS, University of Basel, Spalenring 145, CH-4055 Basel, Switzerland.

e-mail: Lucia.Wick@unibas.ch

Dr. **Pim van der Knaap**, Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland.

e-mail: Pim.VanderKnaap@ips.unibe.ch

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