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BOREAS

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High concentrations of calcite fossil granules produced by earthworms (ECG) have been identified in most of the stratigraphical units along the loess-palaeosol reference sequence of Nussloch (Germany). They are particularly abundant in interstadial brown soils and in tundra gley horizons, the latter reflecting short-term phases of aggradation then degradation of permafrost. These granules are characterized by a radial crystalline structure produced in the earthworms by specific bio-mineralization processes. In our study, we used this biological indicator combined with ^{14}C and OSL dating, and sedimentological parameters to characterize millennial-time scale climatic variations recorded in loess sequences. The approach is based on high-resolution counts of ECG throughout a 17-m-thick loess sequence (332 samples). Strong increases in granule and mollusc concentrations suggest warmer climate conditions during palaeosol formation phases, associated with increasing biodiversity, biological activity and vegetation cover. Decreased granule concentrations occur within primary loess deposits, indicating a strong correlation with palaeoenvironmental conditions and demonstrating the reliability of ECG concentration variations as a new palaeoenvironmental proxy. Finally, this pattern is also recorded in loess sequences located about 600 km westward in northern France demonstrating the large-scale validity of this new palaeoclimatic proxy. 3

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Covering almost all non-glaciated continental areas lower than 500 m between 42 and 52°N, the European Loess Belt represents the most extensive terrestrial archive of the Last Glacial (Pecsi 1990; Haase *et al.* 2007). Its western part is well situated to record the impact of the climatic variations triggered by fluctuations of both North Atlantic oceanic circulation and Fennoscandian sea-ice cover extension propagated eastward by the Westerlies (Renssen *et al.* 2007; Antoine *et al.* 2009). The loess sequences of western Europe provide very detailed and reliable records of climatic and
4 environmental changes of the last 110 kyr in the European Plain (Remy 1968; Antoine *et al.* 2001, 2016; Meijs 2011; Haesaerts *et al.* 2016; Schirmer 2016). Despite the occurrence of some erosion gaps these sequences, made
5 up of complex and cyclic successions of loess units (aeolian deposits) and of soil horizons, have recorded the impact of millennial-scale climatic variability during the Last Glacial (Antoine *et al.* 2009, 2016; Moine *et al.* 2017; Rousseau *et al.* 2017). They also exhibit high
6 sedimentation rates of up to 1 mm per year especially between 30 and 20 ka during the Upper Pleniglacial (Meszner *et al.* 2011, 2013; Antoine *et al.* 2016). Previously based on pedostratigraphical studies, grain-size analysis, terrestrial mollusc assemblages and OSL dating (Antoine *et al.* 2002, 2009; Rousseau *et al.* 2007; Moine *et al.* 2008; Meijs 2011; Schirmer 2012), correlations of palaeosols with Dansgaard–Oeschger events recorded in Greenland ice-cores have recently been improved by radiocarbon dating performed on earthworm calcite granules (ECG; Moine *et al.* 2017). 7

However, as pollen grains are generally not preserved in loess sediments due to their oxidation in this porous sediment, the impact of these millennial climate changes on palaeoenvironment has been until now mainly investigated through the analysis of terrestrial mollusc assemblages (Moine *et al.* 2005, 2008, 2011). The malacological analysis of Nussloch loess sequences revealed a vegetation cover developed on periglacial deposits (Moine 2008) and confirmed that the formation of palaeosols such as tundra gley horizons is associated with moisture increase. In parallel, a new proxy has been discovered in Quaternary deposits: ECG. Surprisingly, the presence of ECG in Last Glacial loess-palaeosol sequences has been found to be common in many regions from western- 8
central Europe (Mazenot 1956; Kerney 1971; Meijer 1985; Becze-Deák *et al.* 1997; Barta 2014; Prud'homme *et al.* 2015; Moine *et al.* 2017).

ECG are composed of large rhombohedral calcite crystals organized in a radial crystalline structure (Canti 1998; Gago-Duport *et al.* 2008). They are produced by a biomineralization process within calciferous glands (also called Morren's glands) located in three pairs on each side of the oesophagus (Darwin 1881). This process starts in the four oesophagus pouches (segments XII and XI) with the secretion of a colloidal 'milky' fluid, which contains amorphous calcium carbonate (ACC) crystals of irregular shape and size ranging from 10 to 50 μm. Then, the milky fluid reaches the two oesophageal pouches in the front (segment X) where the ACC is precipitated into macroscopic crystals of calcium carbonate, which are finally released into the soil through the gut (Briones *et al.* 2008; Gago-Duport *et al.* 2008; Hodson *et al.* 2015). Currently, *Lumbricus* is identified as the most productive genus (Bräm 1956; Canti 1998; Canti & Piearce 2003). *In vitro* experiments showed that this genus releases granules principally at the soil surface in the litter (Canti & Piearce 2003). However, contrary to the species *Eisenia nordenskioldi* and *Dendrobaena octaedra* commonly found in permafrost environments, the *Lumbricus* genus is not considered as freeze-tolerant (Rasmussen & Holmstrup 2002; Holmstrup 2003; Calderon *et al.* 2009). Freeze-tolerant species can endure ice formation in extracellular ~~body~~ due to rapid glucose
9 accumulation in cells. Moreover, *Eisenia nordenskioldi* and *Dendrobaena octaedra* belong to the epigeic class (i.e. living at the surface of the soil) whereas *Lumbricus terrestris* and *Lumbricus rubellus* belong to the anecic and epi-edogenic classes, respectively (i.e. living beneath the soil surface and able to dig burrows). Thus, their life cycle
10 and behaviour ~~cannot be comparable in the same context~~. *Lumbricus terrestris* and *Lumbricus rubellus* are found up to 60 and 65°N, respectively, in the central Russian Plain (Tiunov *et al.* 2006; Meshcheryakova & Berman 2014) and also in southwestern Finland and southern Sweden (Rundgren 1975; Nuutinen & Butt 2009). Although they are often absent from modern permafrost environments
11 (Perel' 1979), adult individuals of both species can
12 survive in soil temperatures as low as −1 °C (Nordström 1975; Rundgren 1975). Moreover, *L. terrestris* is able to overwinter in all life stages and its cocoons (i.e. envelopes protecting the eggs) can survive 1 month in frozen soil (Nuutinen & Butt 2009). Earthworm cocoons resist freezing by cryoprotective dehydration, characterized by a loss of 50% of the mass of their body fluids (Holmstrup 1994). Even though most earthworm species in western Europe were strongly affected by the Last Glacial (Mathieu & Davies 2014), the discovery of abundant granules in palaeosols developed during the Weichselian suggests that a few species ~~have been able~~ to survive in
13 permafrost environment, perhaps even outside refuges. As *Lumbricus* species are currently very abundant in Germany (Jänsch *et al.* 2013) and in the absence of other common large taxa known to produce numerous granules in western Europe (Bräm 1956; Canti 1998), we assume that *Lumbricus* individuals produced the large (≤0.8 mm) granules discovered in the Last Glacial loess sequence of Nussloch.

Previous works showed that ECG: (i) can constitute an ideal material for radiocarbon dating in loess contexts as demonstrated by the new chronology of the Nussloch sequence (Moine *et al.* 2017), (ii) allow the quantification of palaeoclimatic parameters (temperature and precip- 14
itation; Prud'homme *et al.* 2016, 2018) and (iii) can be used as a bio-indicator for palaeoenvironmental reconstructions (Prud'homme *et al.* 2015).

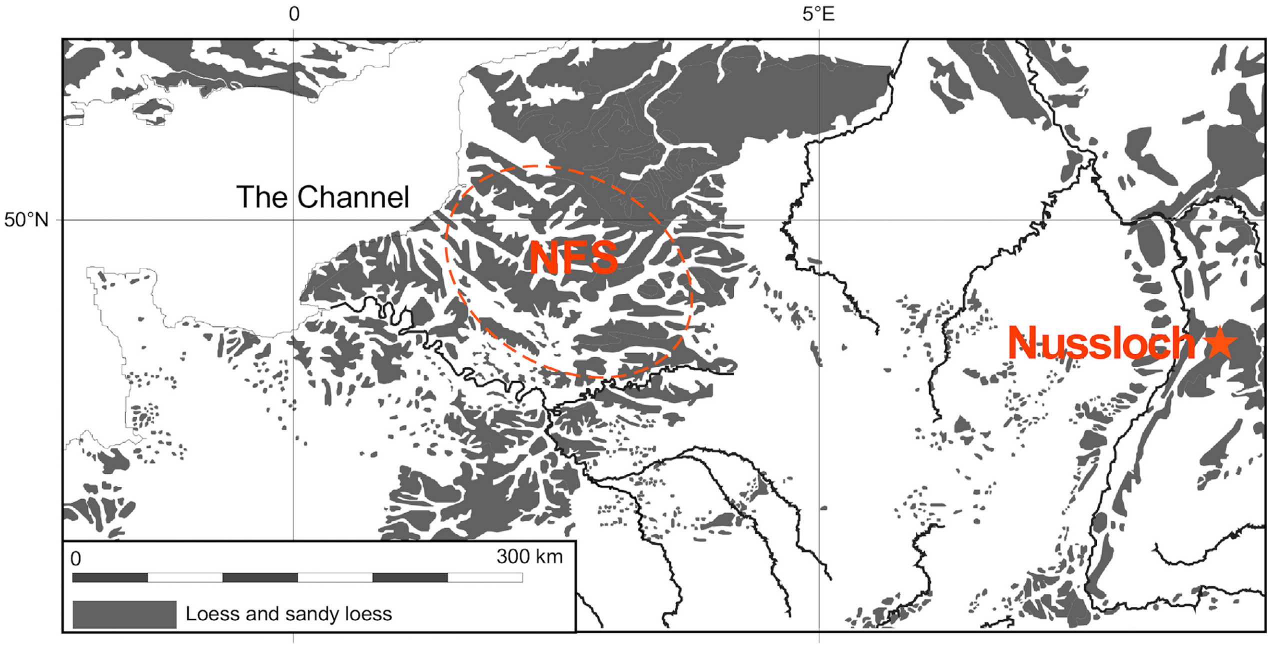
In this paper, we focus on the third point above by presenting the first continuous record of ECG concentration variations from the west European reference site of Nussloch. The 17-m-thick loess-palaeosol sequence encompasses the Weichselian Middle and Upper Pleniglacial from about 55 to 20 ka. The ECG counting profile is compared with high-resolution stratigraphy and grain-size 15
analysis.

Material and methods

Stratigraphy

The Nussloch loess-palaeosol profiles have been studied in an active limestone quarry (latitude 49°18′59″N, longitude 8°43′54″E) located at about 10 km south-southeast of the city of Heidelberg on the eastern flank of the Upper Rhine valley (Fig. 1). The stratigraphy of the former four main profiles (P1 to P4) has already been published in great detail (Antoine *et al.* 2001, 2009). 16
These profiles consist of four sub-sequences attributed to the main chronoclimatic phases of the Last Glacial, i.e. Early Glacial, Lower, Middle and Upper Pleniglacial (Antoine *et al.* 2009). Profile P8, located about 50 m from the reference profile P4 in the same loess greda (i.e. elongated loess ridge forms orientated parallel to the direction of winds; Leger 1990), revealed the same stratigraphical succession and can easily be correlated with the other profiles using specific palaeosol marker horizons. Moreover, a radiocarbon chronology based on 46 dates obtained from ECG has been produced for Nussloch profiles P3, P4 and P8 (Moine *et al.* 2017). This new chronology, combined with some of the previous OSL dates, highlights a very accurate time-framework for the deposition of the Nussloch loess sequence.

According to stratigraphy and sedimentology given in Antoine *et al.* (2009), the 17-m-thick P8 profile is made up of the succession of two main chronoclimatic phases of 18
the Last Glacial: the lower 5 m allocated to the Middle Pleniglacial (from ~55 to 35 ~~ka~~; MIS 3) and the upper 12 m representing the Upper Pleniglacial (from ~35 to 20 ~~ka~~; end of MIS 3 and beginning of MIS 2). The lower part is composed of a succession of two thick boreal brown soils (Lower (GBL) and Upper (GBU) Gräselberger Boden) developed on silty aeolian sands, followed by loess and tundra gley horizons, topped by an arctic brown soil



95 17 *Fig. 1.* Map of the loess and sandy loess cover over western Europe with the location of the Nussloch site and of the northern France sequences (NFS) modified from Haase *et al.* (2007) and Antoine *et al.* (2016).

(Lohner Boden). This part of the record is characterized by an average sedimentation rate of 0.19 mm a^{-1}.

The upper part is characterized by a very high sedimen tation rate (average: 0.93 mm a^{-1}) and by a cyclic alternation of typical calcareous loess and tundra gley horizons. Tundra gley horizons were formed by hydromorphic processes and correspond to active layers of former permafrost events. Thus, these horizons indicate 19 the presence of a former permafrost. This interpretation is supported by observations from northwestern France plateau sections in which large ice-wedge cast networks are systematically connected with tundra gley horizons 20 (Antoine *et al.* 2016). Furthermore, the new radiocarbon chronology of the Nussloch loess sequence (Moine *et al.* 2017) confirms the correlations of both brown soils and main tundra gley horizons with interstadials identified in Greenland ice-core δ^{18}O and dust records.

Sampling strategy

The 17-m-thick Nussloch profile P8 was sampled at high resolution (5-cm-thick) using the continuous column sampling protocol (Antoine *et al.* 2009). ~~Two continuous columns of 332 samples were collected in parallel: one ~5 cm large producing ~300 g samples for grain-size~~ 21 ~~analyses and one ~50 cm large resulting in ~10 L samples (~10–12 kg) for malacological analyses from which granules have been extracted.~~

Grain-size analyses were performed using a Beckman Coulter LS-230 laser particle size analyser following the protocol presented in Antoine *et al.* (2009). Ten grams of homogenized ~~subsamples~~ was first dispersed by addition of sodium hexametaphosphate (5‰), then processed overnight in a rotating agitator, and finally 22 sieved at 160 µm in order to remove the coarse fraction (calcified roots, Fe and Mn concretions and fragments of mollusc shells). Each sample was measured with the Coulter at least three times in order to ~~obtain~~ good reproducibility. The limits of the grain-size classes 23 applied to Nussloch were adjusted using a comparison between classical and laser grain-size analyses from a set of test samples: clay: ≤4.6 µm; coarse silts: 26 to 52 µm; fine sands: 52 to 160 µm. A grain-size index (GSI) reflecting the variations in aeolian dynamics throughout the record has been defined as the ratio between the coarse silt fraction (%) and the fraction of fine silt plus clay (%) (Antoine *et al.* 2009).

ECG were extracted from the malacology samples. After wet sieving (>0.425 mm) of the samples, ECG larger than 0.8 mm were extracted and counted under a binocular microscope to select mainly *Lumbricus* material (Canti 1998; Canti & Piearce 2003). According to Canti & Piearce (2003), this genus has its calciferous 24 glands very well developed and produces the largest granules (with a diameter >0.5 mm).

Results

Variation in ECG concentrations 25

Figure 2 shows that the variation in the ECG concentrations appears to be correlated with the stratigraphy 26

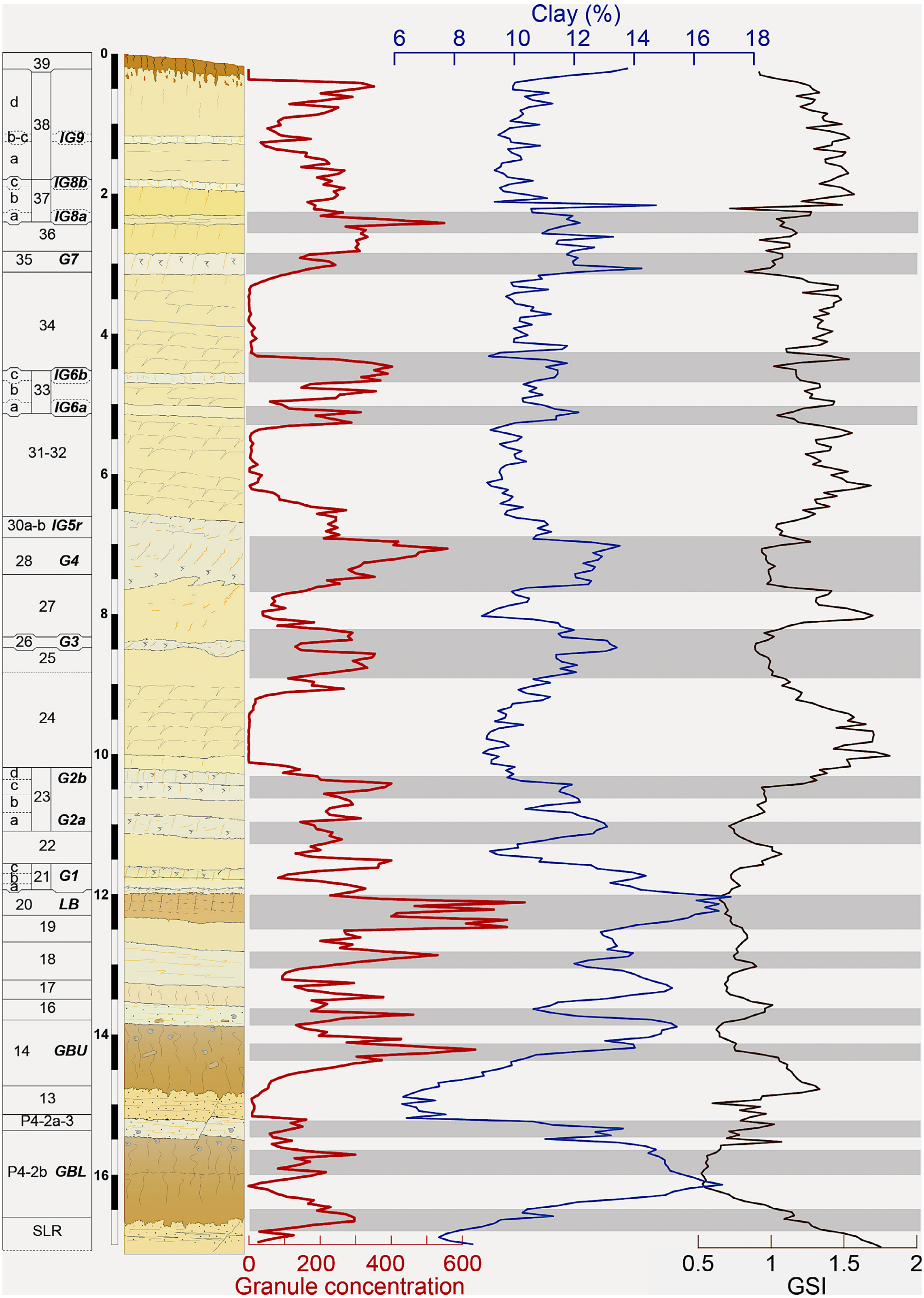


Fig. 2. Pedostratigraphy of the Nussloch profile P8 associated with the earthworm granule concentration (in red), the clay fraction percentage (<4.6 μm, blue) and the grain-size index (GSI, brown). Detailed descriptions of the stratigraphy and lithology are available in Antoine *et al.* (2001, 2009). GBL = Lower Gräselberger Boden (boreal brown soil, Bw horizon); GBU = Upper Gräselberger Boden (boreal brown soil, Bw horizon); LB = Lohner Boden (arctic brown soil, Bw horizon); G = major tundra gley (gelic gleysol horizon); IG = incipient tundra gley; r = reworked.

and with both GSI and clay fraction variations. All the data are available in Table S1.

During the Middle Pleniglacial, the highest ECG concentrations are found in boreal and arctic brown soil (GBU and LB) with more than 600 granules per sample. However, the lower boreal brown soil (GBL) recorded a lower granule concentration (around 200), probably due to its higher coarse sand content. P8 is the first profile that provides evidence of the presence of two horizons in the
27 GBL unit (P4-2b), with a stratigraphical limit found in the section at 16 m. The upper part is characterized by a humic horizon associated with a higher percentage of coarse sand (>160 μm) compared to the lower part. This observation is coherent with the double peak in the granule concentration. This palaeosol probably developed during two interstadials (GI 14 and 13). The maximal ECG concentrations occur between 15 and 30 cm below the surface of these palaeosols.

During the Upper Pleniglacial, the maximal concentrations are observed in tundra gley horizons with values
28 between 130 and 400, whereas homogeneous loess units are associated with extremely low ECG concentrations
29 (between 30 and 100 ~~by 10 L~~). The three laminated loess units are characterized by drastic decreases associated with very low concentrations of large granules (diameter
30 >0.8 mm) between 0 and 10.

Grain-size distribution

The variations in ECG concentration were compared
31 with clay contents and with GSI (ratio between coarse and fine silt+clay). High GSI values imply strong aeolian dynamics and occur within loess units, whereas low GSI values indicate a decrease in dust storms and are correlated within palaeosol formations. GSI highlights relative changes in the aeolian dynamics (Rousseau *et al.* 2007; Antoine *et al.* 2009). Throughout the profile P8, GSI varies from 0.5 to 1.9 (Fig. 2). Palaeosols are characterized by the lowest values whereas the highest ones are associated with loess units.

The clay percentage is affected by two processes: (i) weathering of loess leading to soil formation and (ii) variations in aeolian dynamics (highest values corresponding to phases of low sedimentation rates). The clay fraction varies between 6.3 and 17.2% (Fig. 2). The lowest value is found in unit 13, whereas the highest value is found in the Lohner Boden (unit 20). During the Upper Pleniglacial, the tundra gleys are characterized by higher clay percentages and lower GSI values compared to loess units. The grain-size analyses of profile P8 confirm the cyclic pattern of the loess-palaeosol sequence pedostratigraphy as already shown by Antoine *et al.* (2009) and Rousseau *et al.* (2007). Moreover, the comparison between the variations in ECG concentration and in clay
32 percentage shows a medium correlation ($R = 0.6$) as illustrated by Fig. 2.

Discussion

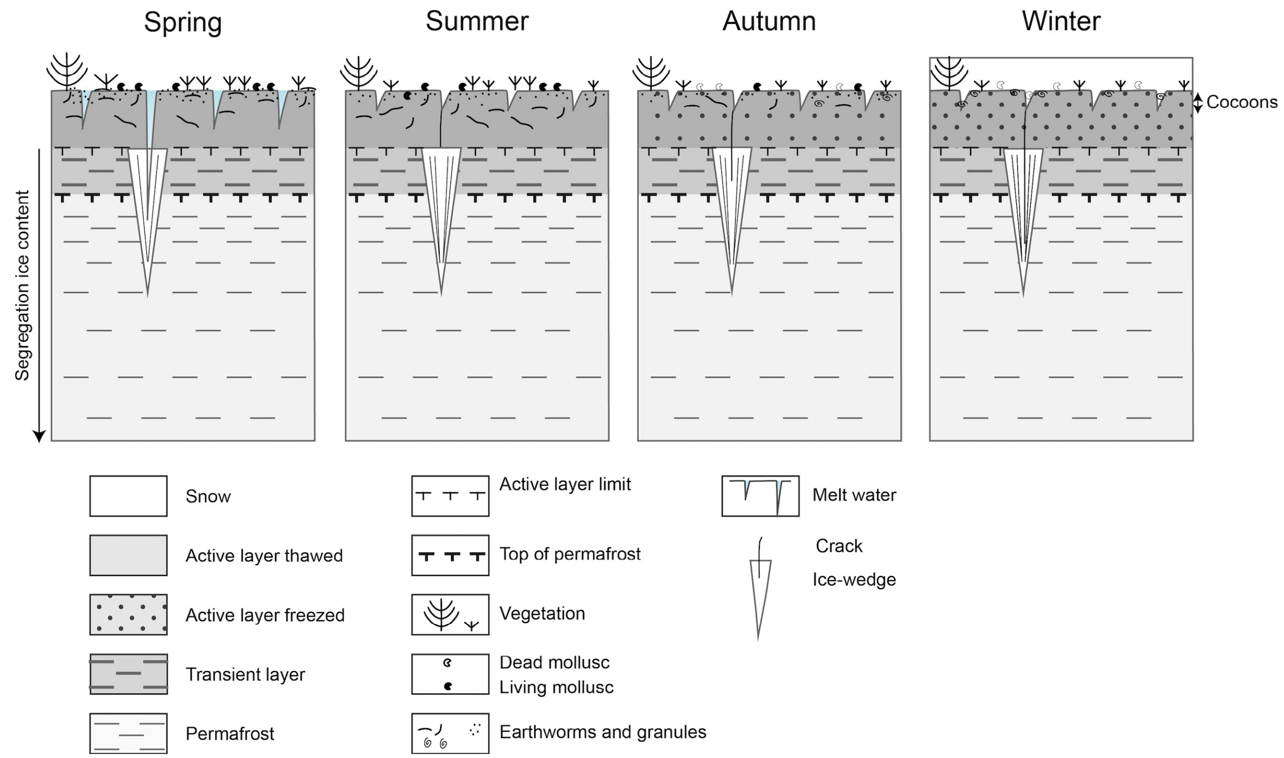
Survival strategy and seasonal activity of earthworms during the Last Glacial

The discovery of high ECG concentration in palaeosols formed during the Last Glacial and the good correlation with the pedostratigraphy demonstrate the presence and the survival of earthworm species during this period in western Europe, preferentially during interstadials, as already observed in northern France loess sequences (Prud'homme *et al.* 2015). In this study, a more complete record of ECG concentration variations has been obtained between ~55 and 20 ka due to the almost continuous sedimentation and high sedimentation rate of the Nussloch sequence, especially for the Upper Pleniglacial (12 m). High large granule concentration in the tundra gley horizons (active layer of a former permafrost) suggests the presence of the earthworm genus *Lumbricus* (*terrestris* and *rubellus*) in permafrost
~~environment~~. By contrast, the very low concentration or 33
even the lack of large ECG in loess units indicates a
drastic decrease in earthworm activity, but not a total 34
absence of earthworms as a few small granules (0.5 to
0.8 mm) can be found. 35

According to the literature, *Lumbricus* species are not considered as freeze-tolerant, and they are not found in modern permafrost (Perel' 1979; Holmstrup 2003; Calderon *et al.* 2009). However, as already described in the Introduction, *Lumbricus* is the only earthworm genus
able to produce a high quantity of large granules (Bräm 36
1956; Canti 1998; Canti & Pearce 2003), and this genus is found in Russia and in Scandinavia (Tiunov *et al.* 2006; Meshcheryakova & Berman 2014). The activity of earthworms and the production of granules are directly linked to both soil temperature and humidity and are thus influenced by seasonal climate fluctuations. Nowadays, the maximum activity of earthworms is observed during spring and autumn ~~and can stop the rest of the~~
~~year~~ (Satchell 1967). Experimental studies on ~~natural~~ 37
~~environment~~ indicate that *Lumbricus terrestris* are inac-
tive when the soil is frozen (Nordström 1975; Rundgren 38
1975); however, adult individuals are able to survive and their cocoons (egg matrix) are cryo-resistant (Holmstrup & Zachariassen 1996; Meshcheryakova & Berman 2014). In Fig. 3, a conceptual model is proposed to explain how earthworms were able to survive during the Last Glacial
in a permafrost environment ~~in function of the seasons~~: 39 40

- Spring is associated with the thawing of the upper horizon of the permafrost (active layer), develop-
ment of vegetation and increases in biological activity. 43
Earthworm populations are growing and their activity is basically concentrated at the surface (feeding). In addition, they are confined to the upper part of the active layer (~15–30 cm thick), which is coherent with
the thickness of the tundra gley horizons ~~on the field~~ 44

COLOR



41 *Fig. 3.* Schematic model of the different earthworm activity phases in a permafrost environment depending on the season. ~~See on the text for the~~
42 ~~description of the figure~~.

(French 2007; Burn 2012). The conditions are favourable for the production of granules.

- 45 In summer, although the conditions are drier, *Lumbricus terrestris* are still active (Nordström 1975). The earthworms are mainly found in the upper 5 cm of the soil due to the high proportion of juveniles, which are not able to dig in the deeper layers (Rundgren 1975).
- In autumn, granule production becomes lower, and the earthworms start to overwinter. The cryo-resistant 46 cocoons are already produced (Holmstrup & Zachariassen 1996) and are mainly distributed in the upper 7.5 47 cm of the soil (Gerard 1967).
- In winter, the biological activity stops and the earthworms are in diapause. The snow cover should be thick enough to protect the soil from extreme 48 temperatures (French 2007). The earthworms are confined to the interface between the thick snow cover 49 and the topsoil. The cocoons protect the eggs until 50 they hatch during the next spring, when the conditions become milder (Tiunov *et al.* 2006; Meshcheryakova & Berman 2014).

The earthworms are thus confined to the active layer of the permafrost, greatly reducing the mixing of the 51 granules ~~through depth~~, ~~allowing an accurate chronological approach of these horizons using ECG ^{14}C dating~~ 52 (Moine *et al.* 2017). Furthermore, field observations and thin sections indicate an absence of galleries and hibernation chambers in these horizons as the earthworms remain mainly at the surface (Rundgren 1975). More- 53 over, the rate of active horizontal movements (due to locomotion) varies amongst species, but is limited to 14 m a^{-1} in the most favourable conditions, and is generally around 4 m a^{-1}(Eijsackers 2011; Caro *et al.* 2013). The effect of dryness on earthworm movements has not been studied so far, yet it is indeed an interesting question. However, it has been shown for a long time that earthworms go into quiescence, ~~a form of resistance~~, 54 when the soil dries out (Satchell 1967; Bouché 1972). Bearing in mind that dispersal is very costly in terms of survival, due to predation and other risks, it is more likely that earthworms enter into ~~such a form of resistance~~ rather than dispersing during unfavourable 55 conditions.

Comparison between ECG concentration, pedostratigraphy and grain-size distribution

The good correlation between ECG concentration, clay percentage variations and the stratigraphy (Fig. 2) confirms that earthworms produced the granules during the formation of palaeosols and not after. Granules are thus contemporaneous with the horizons in which they are found. Additionally, the variations in mollusc concentration in the profile P3 of Nussloch (Moine *et al.*

2008) show a similar pattern to the ECG variations, especially during the Middle Pleniglacial. The boreal (GBU) and arctic (LB) brown soils as well as the major tundra gleys are associated with the highest ECG 56 abundances (up to 700) and with high molluscan species diversity and individual concentration. ~~As already observed in the counting of the ECG in P8~~, the boreal brown soil (GBL) is characterized by lower molluscan 57 abundances than GBU and LB in P3. The increase in molluscan species diversity in these palaeosols indicates a densification of the vegetation cover from steppe to a herb/shrub tundra environment during the Lower–Middle Pleniglacial transition (Moine *et al.* 2005).

The vertical distribution of ECG through the palaeosols between about 55 and 35 ka differs from that in the present-day soils (Fig. 4). In the brown soils and tundra gley horizons, the maximum number of ECG is not found at the surface of the soil but 15 to 30 cm below. However, in present-day soils, earthworms (especially *Lumbricus* 58 *terrestris* and *L. rubellus*) need a land surface to feed and they produce a high concentration of granules within 59 the litter layer (Canti & Piearce 2003; Canti 2007). This pattern of the ECG concentration suggests that boreal and arctic brown soils result from accretionary soil processes (upbuilding soils; Nikiforoff 1949; Almond & Tonkin 1999) associated with a low aeolian sedimenta-60 tion, which is contemporaneous with weathering processes. This hypothesis is also confirmed by ~~the distribution of the mollusc concentration through the~~ 61 ~~Middle Pleniglacial palaeosols in Nussloch~~ (Moine *et al.* 2008, 2011). Indeed, most of the mollusc species found in Nussloch are surface species and do not bury more than 5 cm in depth to hibernate (Moine *et al.* 2008). Therefore, loessic sedimentation did not stop completely 62 but only reduced during the palaeosol formation.

Major and incipient tundra gley horizons were developed during the Upper Pleniglacial (Fig. 2). The incipient tundra gley horizons described in the Nussloch loess profiles are associated with high ECG concentrations comparable to major tundra gleys and with an increase in the clay content, especially for IG5, IG6 and IG8a (Fig. 2, units 30a–b, 33a–c, 37a). This pattern is not recorded in the number of individual molluscs, although a decrease in the diversity and a slight increase from 20 to 30% in the proportion of *S. oblonga* is observed. The comparison between the stratigraphical observations 65 and the variations in ECG concentration suggests that incipient tundra gleys might correspond to rapid and very short climate improvements (≤0.3 ka), less intense than the interstadial phases. Based on recent ECG radiocarbon chronology, incipient tundra gleys appear to be correlated with significant decreases in Greenland ice-core dust records (Moine *et al.* 2017). Moreover, a slight shift between pedostratigraphical limits, ECG concentrations and clay percentage is observed very clearly for the incipient tundra gleys IG5, IG6 and IG8 66 and for the major tundra gleys G2, G3 and G4 (Fig. 2). Thus, the increases in ECG concentration and clay percentage seem to record the beginning of a warming 67 phase, associated with an increase in edaphic humidity and a reduction in the sedimentation rate, slightly below the stratigraphical limits, i.e. preceding the development of the tundra gley horizons. 68

By contrast, the low concentration of large granules and the absence of molluscs in loess units indicate that the conditions were too extreme for earthworm and mollusc activities. The homogeneous loess units (especially units 22 and 23b) are associated with low ECG concentrations (50–150 granules), but not as low as the laminated loess units, in which they are close to zero ~~and not significant~~ (0–10 in 10 L samples). 69

This pattern suggests that the climatic conditions during the deposition of homogeneous loess units were not extreme enough (cold, dry and windy) to affect the activity of the earthworm population, in contrast to the mollusc population. Earthworms were thus proba- 70 bly more resistant to extreme conditions than molluscs 71 during the extreme cold phases of the Last Glacial. Indeed, whereas terrestrial molluscs live mainly at the surface of the soil, earthworms live in the soil and feed at the surface. This difference can explain the two patterns of these two ~~proxies,~~ especially during the Upper 72 Pleniglacial. Besides, the deposition of the laminated loess units (units 24, 31–32 and 34) is characterized by a high sedimentation rate (≥1 mm a^{-1}) and by the occurrence of thin sand beds resulting from dust storms able to rework sand grains from the alluvial plain of the Rhine and niveo-aeolian processes (Antoine *et al.* 2009). An 73 abrupt decrease in ECG concentration is systematically observed in these facies in the Nussloch loess sequence ~~(0 to 10 granules~~) associated with a decrease in the 74 percentage of clay content and an increase in the GSI. These observations highlight an enhancement of the wind and aeolian dynamics coupled to extreme climatic conditions, which increase the desiccation of the surface. The correlation between the pedostratigraphy of the loess sequence and the NGRIP dust data suggests that these particular horizons are contemporaneous with the Heinrich Stadials HS 3 (around 30 ka) and HS 2 (between 26 and 24 ka) (Rasmussen *et al.* 2014; Moine *et al.* 2017). Heinrich Events, primary ~~highlight~~ in the Atlantic marine core (Heinrich 1988; Bond & Lotti 1995), are characterized by a cold and arid climate on the continent 75 (Fletcher *et al.* 2010; Harrison & Sanchez Goñi 2010; Menviel *et al.* 2014). The comparison between the Heinrich layer in the Atlantic marine core and the Greenland ice-core suggests that the Heinrich Events are contemporaneous with dust peaks in the Greenland ice-core (Fig. 5). Thus, variations in ECG concentrations through loess-palaeosol sequences can be considered as a new proxy of relative variations in aridity. Moreover, ~~the impact of extreme cold events and wind intensity can also be recorded when the ECG concentration is close to 0 during Heinrich Events~~. The same signal (very low to 76

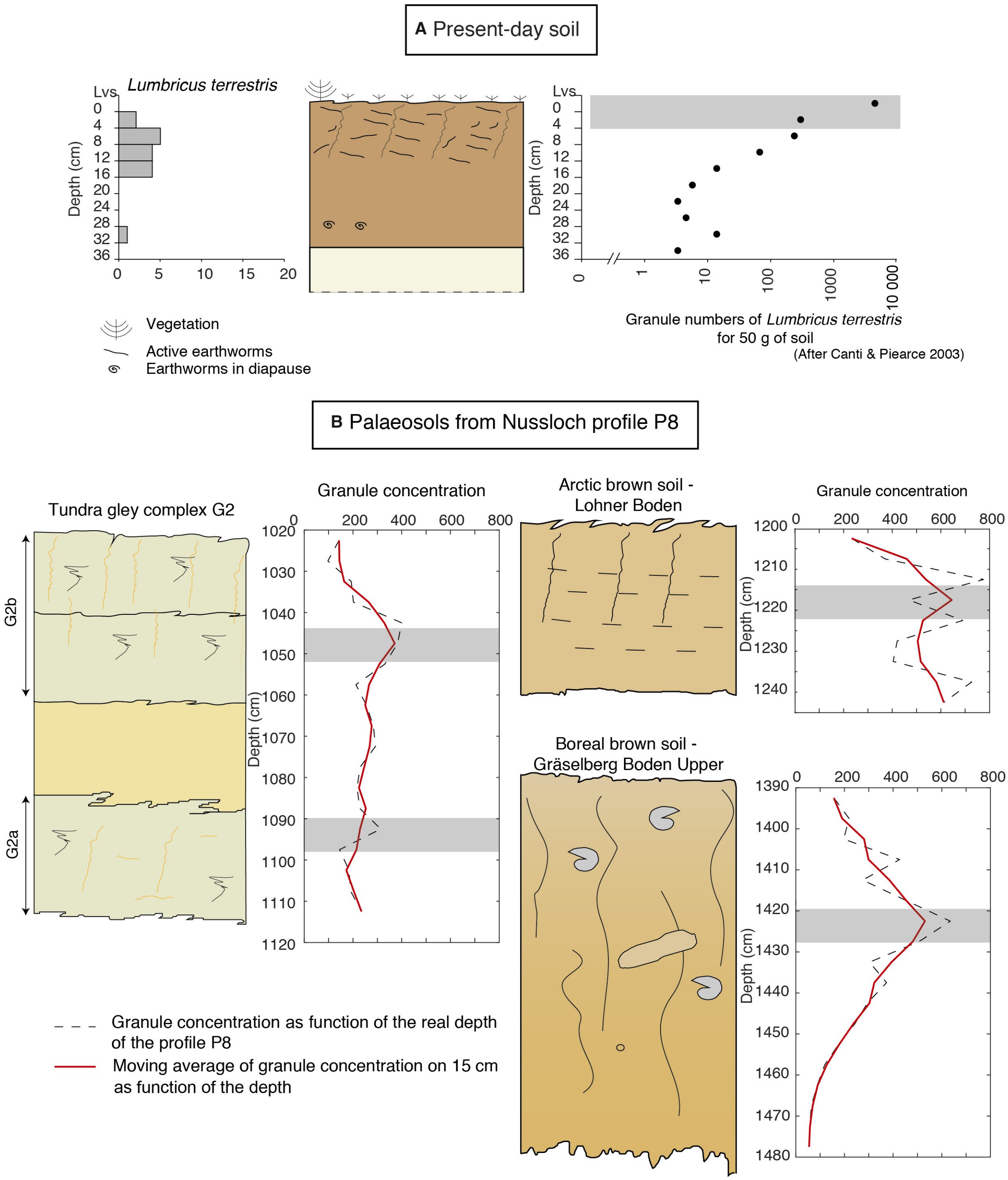


Fig. 4. Distribution of the ECG concentration through (A) present-day experimental soil and (B) three types of palaeosols from the Nussloch loess profile. The distribution of granules through the present-day experimental soil is associated with the distribution of the number of *Lumbricus terrestris* as a function of depth. The granules were extracted from 50 g of the soil and around 10 000 granules were found in the litter sample (Canti & Piearce 2003). The ECG were extracted from 10 L of sediment every 5 cm through the tundra gley horizons and arctic and boreal brown soils.

zero ECG concentration) is recorded 600 km away in two northern France loess sequences (Fig. 1) for the same time-span (around 30 ka), suggesting that variation in ECG concentrations can be used to evidence the response of west European environments to large-scale rapid climatic changes.

Comparison with Greenland records

The radiocarbon chronology performed on the ECG confirmed that the two brown soils formed during the Middle Pleniglacial (GBU and LB) can be correlated with Greenland interstadials (GI) 12 and GI 8/7c, and that major tundra gleys G1, G2, G3, G4 and G7 can be correlated with GI 6, GI 5, GI 4, GI 3 and GI 2, respectively (Moine *et al.* 2017). During this time period, the Greenland interstadials GI 12 and GI 8 are the longest interstadials (2700 and 1700 years, respectively), whereas the duration of the GIs correlated with the development of tundra gley horizons are shorter, between 600 and 200 years. The temperature reconstructions performed on NGRIP indicated an increase between 8.5 °C (GI 2) and 15.5 °C (GI 7), with no particular difference between long and short interstadials in this arctic area (Landais *et al.* 2004; Capron *et al.* 2010; Kindler *et al.* 2014). Moreover, palaeoclimate parameters (temperature and precipitation, Fig. 5) have been estimated from oxygen and carbon stable isotope analyses performed on ECG (Prud'homme *et al.* 2016, 2018). During the formation of GBU, the air temperature for the five warmest months was 13.0±4.1 °C and the mean palaeoprecipitation was 287 +223/−161 mm a^{-1}, whereas during the formation of the Lohner Boden, the temperature of the warmest season was 11.7±3.6 °C and the mean rainfall was 322 +236/−171 mm a^{-1} (Prud'homme *et al.* 2016, 2018). The palaeoenvironmental reconstructions from the coastal Atlantic marine

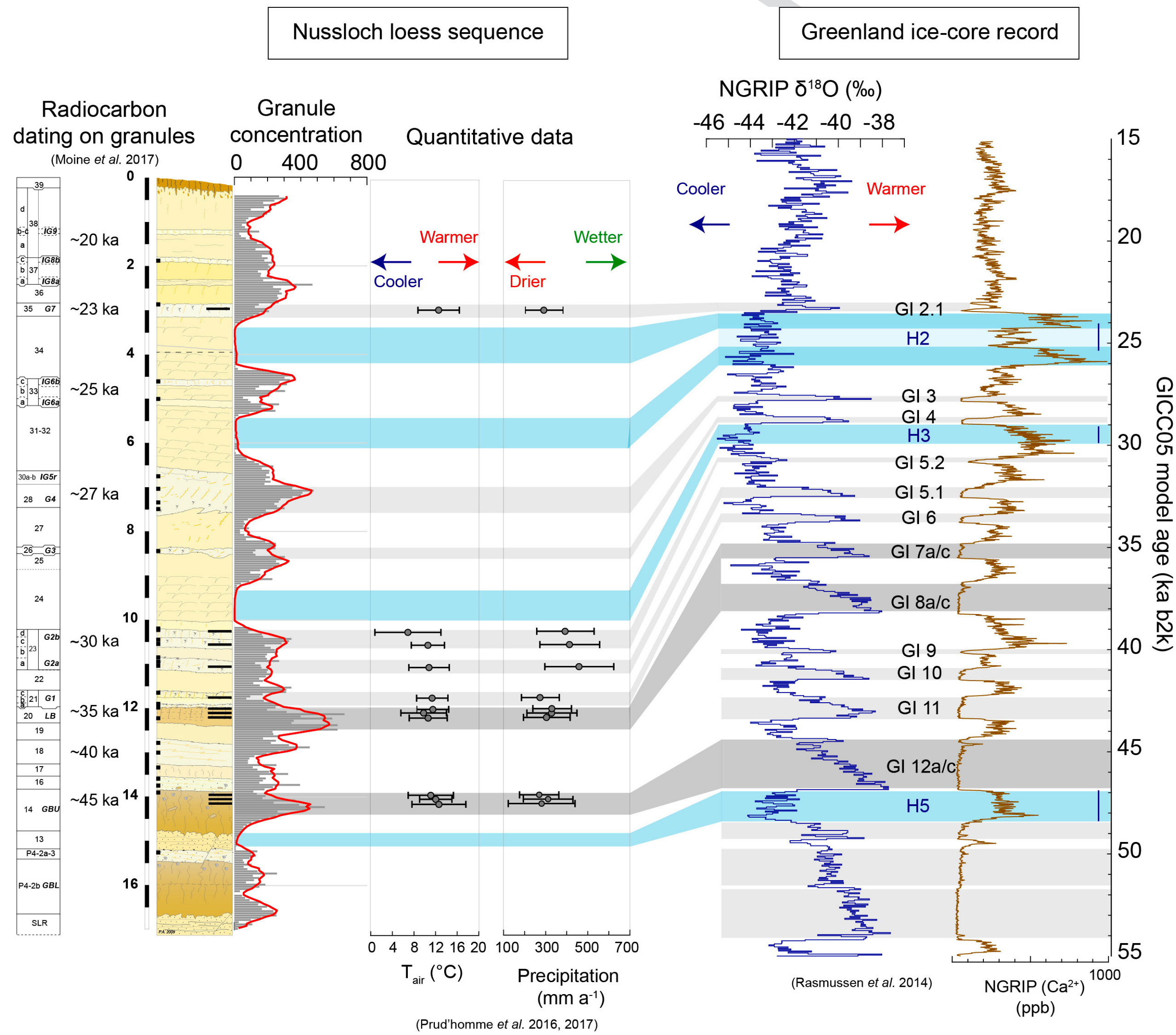


Fig. 5. Correlation between ECG concentration and quantitative palaeoclimate parameters (temperature and precipitation; Prud'homme *et al.* 2016, 2018) of the Nussloch loess sequence with the Greenland ice-core record (Rasmussen *et al.* 2014) and the Heinrich events (Rasmussen *et al.* 2016) based on the ECG radiocarbon chronology of the loess sequence (Moine *et al.* 2017).

79 core MD04 2845 next to the French coast and located above 45°N indicate that GI 12 is characterized by a mild and moderately humid environment with mainly *Pinus* forest whereas GI 8 is still mild but less humid with a vegetation represented by grassland and dry shrubland (Fletcher *et al.* 2010).

The difference in humidity between GI 12 and GI 8 recorded in Nussloch loess sequence is also confirmed by the pedostratigraphy. The LB is an arctic brown soil with the presence of cryostructures (platy structure indicating ice-lensing processes), which indicate more humid conditions than in the boreal brown soils (GBU) (Antoine *et al.* 2009). Furthermore, during the Upper Pleniglacial, palaeoclimate data indicate that tundra gley horizon G2a/b was formed during mild and humid conditions (Fig. 5). The air temperature of the warmest season was 9.4±4.3 °C and the mean annual precipitation was 425 +273/−201 mm a^{-1}. These climate conditions are supported by (i) the very high proportion (more than 50%) of the hygrophilous mollusc taxon *Succinella oblonga* (Moine *et al.* 2005, 2008) and by (ii) more intense hydromorphic features, such as ~~stronger~~ reduction, greenish colour and more developed iron oxide precip-
80 itation around root tracks (Antoine *et al.* 2009). The two
81 horizons G2a and G2b of tundra gley G2 are respectively correlated with GI 5.2 and GI 5.1 (Moine *et al.* 2017). This interstadial (600 years) is characterized by an increase of +12.5 °C prior to the Heinrich Event H3 (Kindler *et al.* 2014; Rasmussen *et al.* 2014). Wetter conditions are also recorded ~~on~~ the laminated Eifel maar
82 sediments in Germany, where four flooding events were discovered around 30 to 31 ka, suggesting intense spring snow-melt events (Sirocko *et al.* 2015). This period (around 31–30 ka) corresponds to the first step of the maximal expansion of the Fennoscandian ice sheet, implying an increase in moisture ~~conditions~~ in NW
83 Europe (Hardt *et al.* 2016; Hughes *et al.* 2016). This time-span is also characterized by the first considerable
84 increase in typical loess deposition throughout north-western Europe (Antoine *et al.* 2016).

Conclusions

The first continuous record of the variations in large ECG concentration through the Nussloch loess sequence led to the discovery of very high granule concentrations in boreal and arctic brown soils and tundra gleys horizons, whereas loess deposits are distinguished by very low values that are even close to zero in laminated loess units. Generally, the variation in ECG concentration is well correlated with stratigraphical boundaries and variations in clay percentages, suggesting a link with palaeoclimate and palaeoenvironmental changes. Nevertheless, the maximal abundance of ECG is not found at the surface (as in the present-day soil profile) but 15 to 30 cm deeper. This observation suggests that loess sedimentation was not null during the formation of boreal and arctic brown soils and tundra gleys horizons. Moreover, the high concentration of large granules in the incipient tundra gley horizons indicates that these units may be associated with rapid and short climate improvement but less intense than that during the interstadial phases, which is favourable to earthworm activity. However, the absence 85
of terrestrial molluscs in these horizons suggests that 86
earthworms are more resistant to periods of marked climatic stress (cold and arid conditions) as they can protect themselves by burrowing into the soil, especially in very exposed conditions such as at the top of the Nussloch loess gredas.

Furthermore, the good correlation between the ECG concentration and the clay content in tundra gley horizons suggests that the beginning of the warming associated with the increase in humidity is ~~anterior~~ to the
formation of the stratigraphical units and thus to the 87
functioning of the active layer.

The comparison between the high concentration of ECG in palaeosols and the radiocarbon dating confirmed that boreal and arctic brown soils and tundra gley horizons were formed under ~~milder~~ climatic conditions
(interstadial events) associated with the development of 88
biodiversity.

Finally, the three drastic decreases in ECG concentration ~~suggest that they are~~ contemporaneous with peaks
of dust recorded in the Greenland ice-core associated 89
with Heinrich Events (H3 and H2). Thus, the absence of large ECG can be interpreted as a new indicator of aridity through the loessic sequence of Nussloch, even though the role of potentially very low temperatures and the increase in wind intensity during these three cold stages
should also be considered. This approach could therefore 90
highlight in the future, climatic oscillations that are hardly identifiable in other contexts. Moreover, the same pattern is observed in two loess sequences of northern France (600 km to the west) in the same period (30 ka), suggesting a global aridity signal over western Europe. In
the future, an investigation of variation in the ECG 91
concentration at the top and at the sides of a greda in loess-palaeosol sequences formed in gentle topography could provide information about the migration of earthworms and their possible refuges during the Last Glacial.

The comparison between ECG concentration, grain-size variations, palaeoclimate data and radiocarbon dating confirms that ECG can be used as a new palaeoenvironmental and palaeoclimate proxy of the Last Glacial in
continental environments. Therefore, it can help to better 92
understand the response of terrestrial archives to the millennial climate variations highlighted in ice-cores.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at http://www.boreas.dk.

Table S1. Numerical data of granule counting and granulometry analysis (clay content <4.6 µm, coarse sand content >160 µm) of Nussloch profile P8.