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Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates

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A B S T R A C T

Local environmental conditions under dense canopy are known to result in depletion in ^{13}C abundance in plants compared to an open land context. This canopy effect has been observed in tropical as well as in mid-latitude forest ecosystems. However, the impact of the canopy effect on tissue ^{13}C abundance of temperate and boreal forest-dwelling herbivores has not been thoroughly explored. Nevertheless, the canopy effect has been suggested to explain a decrease of about 3‰ in collagen $\delta^{13}C$ values in ancient large herbivores from western Europe during the forest expansion of the Late-Glacial–Early Holocene period (ca. 15,000–6000 cal BP). Some papers have considered the ^{13}C decrease in large herbivore as the main result of global change in atmospheric CO_2 content. A detailed review of $\delta^{13}C$ values of large herbivores (reindeer, red deer, roe deer, and bison) from open and closed environments from high and mid-latitudes confirm that the canopy effect observed in plants is passed on to their consumers. In the Paris Basin, the decline in $\delta^{13}C$ values of large herbivores at the Late-Glacial/Early Holocene transition around 10,000 years BP appears to be different according to the considered species, namely red deer, roe deer, and large bovines (bison and aurochs). Moreover, differences in the pattern of decrease in $\delta^{13}C$ values are observed in red deer between French northern Alps and French Jura. These differences among species in their isotopic response through time for a given geographical location, and within species from different locations, suggest variance in ecological responses of species that are associated with the relative use of forested habitat. As a result, ^{13}C abundances in collagen can be considered as a direct tracker of the degree of closure of the habitat of ancient herbivores.

1. Introduction

Habitat use and dietary preferences of ancient herbivores is an important question in palaeobiology. In tropical contexts, the use of carbon isotopic signatures ($\delta^{13}C$) of modern and fossil herbivore tissues is nowadays routinely used to document these issues, since herbaceous plants in open environments and herbaceous and arboreal plants from forested contexts use different types of photosynthesis, C_4 versus C_3, which exhibit very distinctive carbon isotopic signatures (e.g. Ambrose and DeNiro, 1986; van der Merwe et al., 1990; Vogel et al., 1990; Cerling et al., 1998). In boreal and temperate ecosystems, where C_4 plants are practically absent, C_3 plants exhibit isotopic contrasts according to environmental conditions (see reviews in Tieszen, 1991; Heaton, 1999; Dawson et al., 2002). Variation in $\delta^{13}C$ values in C_3 plants has been observed in response to soil moisture, low humidity, irradiance, temperature, nitrogen availability, salinity, and atmospheric CO_2 concentration. Despite these numerous factors influencing ^{13}C assimilation by C_3-plants, some systematic patterns are observed between different plant assemblages. One of those patterns is the so called "canopy effect" that corresponds to a vertical gradient in the $\delta^{13}C$ values of forest trees, with high $\delta^{13}C$ values at the top of the canopy and low values at the bottom, and to a ^{13}C depletion in plants growing under forested closed canopy relative to the same plant type subject to more open growing conditions (e.g., reviews in Broadmeadow and Griffiths, 1993; Heaton, 1999). This ^{13}C depletion in plants growing under forested closed canopies may be linked to the combination of two factors: (1) atmospheric CO_2 available to plants in poorly ventilated understory is ^{13}C depleted relative to the general atmosphere as the result of CO_2 recycling from leaf litter (e.g. Schleser and Jayasekera, 1985; Gebauer and Schulze, 1991; van der Merwe and Medina, 1991), (2) a CO_2 concentration gradient and light attenuation under the forest canopy leads to depleted ^{13}C abundances in understory plants due to change in photosynthetic activity and

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stomatal conductance (e.g. Francey et al., 1985; Ehleringer et al., 1986; Gebauer and Schulze, 1991; Broadmeadow et al., 1992). Some authors also invoke a higher water availability for plants growing under canopies relative to plants growing in more exposed sites (Broadmeadow et al., 1992; Brooks et al., 1997). Consequently, the intensity of canopy effect is expected to depend on the characteristics of the canopy. General trends are that the more complex and denser the canopy, the greater the extent of light reduction and the degree of recycling of respired forest floor CO_2 within the understory layers (France, 1996). For a significant ^{13}C depletion to be observed in arboreal plant formations, two conditions need to be fulfilled: CO_2 produced by plant respiration is confined and the gradient of CO_2 is not dissipated by wind turbulence (e.g., Broadmeadow and Griffiths, 1993; France, 1996; Roche, 1999), and the light attenuation is sufficient thanks to a high Leaf Area Index (Broadmeadow and Griffiths, 1993; Buchmann et al., 1997).

The "canopy effect" causing changes in ^{13}C abundances of plants is expected to be passed on to herbivores feeding on understory vegetation. Indeed, some studies tentatively established links between ^{13}C abundances in animals and the canopy effect. For instance, depleted ^{13}C abundance has been shown in tissues from elephants living in tropical forest compared to those living in savannah (van der Merwe et al., 1990; Vogel et al., 1990), but the occurrence of C_4 plants with $\delta^{13}C$ values as high as −12‰ in savanna grass may contribute to an exaggeration of the difference between the $\delta^{13}C$ values of both populations. Also, the more negative $\delta^{13}C$ values measured in South American monkeys living in closed canopy forest compared to those living in more open environments presented by Schoeninger et al. (1997) may be partly due to differences in dietary specialisation between the considered species. One recent attempt to document canopy effect in red deer collagen $\delta^{13}C$ values based on the comparative study of five European populations from C_3 contexts remains unconvincing (Stevens et al., 2006), but this outcome is more due to the difficulty of finding red deer populations unaffected by anthropogenic interferences rather than on the absence of the canopy effect (see discussion in the present paper). Finally, there is no ideal example showing a significant difference in $\delta^{13}C$ values for two populations of the same species, one living under a closed-canopy forest and the other one living in a more open C_3 environment.

The potential of ^{13}C measurement of herbivore tissue for tracking the degree of closure of habitat is an important question to address. Indeed, climatic fluctuations in the past has led to major vegetation changes, as it was the case of the transition from Late-Glacial to Early Holocene (ca 15,000–6000 years cal BP) in western Europe. As a result of global climatic warming, the vegetation composition changed drastically from steppe–tundra dominated by grass and herbaceous dicotyledones to temperate dense deciduous forest through intermediate stages of open boreal-like forests as reconstructed from pollen records (e.g. Amman and Lotter, 1989; Beaulieu et al., 1994a,b). Among game species, arctic-steppe species like reindeer (*Rangifer tarandus*) and bison (*Bison priscus*) were gradually replaced by temperate species like aurochs (*Bos primigenius*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) after a period of coexistence during the Late Glacial Interstadial. Late-glacial and Early Holocene major change of landscape provoked a change in the subsistence strategies of prehistoric populations linked to the change in the habitat of their game. Therefore, it is of high interest to define the degree of opening of the habitat of ancient herbivores using their $\delta^{13}C$ values. In this context, the decrease in herbivore ^{13}C abundances during Late-Glacial–Early Holocene transition in western Europe has been attributed to the increasing forest cover at this time (Drucker et al., 2003; Noe-Nyggard et al., 2005). In contrast, some papers consider that the decrease in ^{13}C abundance of herbivores during this period essentially results from an increase in CO_2 concentration in the atmosphere along with a decrease in plant ^{13}C abundance (Richards and Hedges, 2003; Stevens and Hedges, 2004).

We wanted to determine whether the canopy effect is a convincing explanation for the observed decrease in carbon-13 abundance in herbivores during the Late-Glacial/Early Holocene transition. For this purpose, we address the following two questions. First, in modern boreal and temperate environments, can the canopy effect result in depletion of ^{13}C abundance in tissues of large herbivores regardless of their forage preferences? Second, during the Late-Glacial and Early Holocene, did the pattern and timing of the decline in ^{13}C abundance in herbivores vary according to species and geographical location? Such variation is expected if a local parameter, such as canopy effect, rather than a global parameter, such as atmospheric CO_2 content, is primarily involved in the herbivore ^{13}C depletion.

2. Background information on habitat and dietary specialisation of the studied ruminants

The present study includes carbon isotopic data from modern representatives of five herbivore species, all belonging to the Artiodactyla and more specifically to the Ruminantia. Three of them are cervids: reindeer (*Rangifer tarandus*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*). The two others are bovini: American bison (*Bison bison*), and European wisent (*Bison bonasus*). These species have been selected on the basis of several factors: (1) a similar digestive physiology based on rumination, (2) well-monitored populations with minimal anthropogenic interference, living under closed-canopy and more open conditions (reindeer, roe deer, red deer), (3) remains of such taxa are often abundant in the Late-Glacial and/or Early Holocene archaeological sites from France. Two extinct bovini are also considered here, steppe bison (*Bison priscus*) and aurochs (*Bos primigenius*), and ancient domestic cattle (*Bos taurus*), which was used for comparison with its wild relatives during the Early Holocene.

Reindeer (*Rangifer tarandus*) is a medium-sized deer adapted to arctic and boreal environments, with a circum-polar modern distribution. In Canada, two main ecotypes are recognized, one dwelling essentially in the arctic tundra, the barren-ground caribou, the other one dwelling all year long in old-growth mature boreal forest, the woodland caribou (e.g. Kelsall, 1968; Russell, 1998). Wild reindeer from Siberia dwell in varying habitats, from arctic tundra to more forested environments. Reindeer are mixed feeders, quite plastic in their food habits. They consume a large range of vascular plants, including shrub leaves, forbs, and graminoids (grass, carex). In contrast with other herbivores, reindeer have the ability to sustain primarily on large amounts of lichen, in tundra as well as in boreal forest (e.g., Flerov, 1952; Kelsall, 1968; Lindgren et al., 1983; Rettie et al., 1997; Russell, 1998; de Bellefeuille, 2001). Living outside the geographical range of cultivated areas, caribou from mainland North America is one of the few deer with populations dwelling in contrasted habitats with similar diet composition, but without significant anthropogenic interferences. It is therefore a good candidate to test the impact of canopy effect on $\delta^{13}C$ values. Nonetheless this species disappears from the fossil record at the end of the Late-Glacial, around 12,000 years ago in France (e.g., Bridault et al., 2000), whereas it is still documented during the last cold oscillation of the Late-Glacial in Belgium and northern Germany (Charles, 1993; Baales,1996) and at the beginning of Holocene in Great Britain and Southern Scandinavia (e.g., Coard and Chamberlain, 1999; Ukkonen et al., 2006; Aaris-Sorensen et al., 2007).

Red deer (*Cervus elaphus*), called elk in Eurasia and wapiti in North America, is a large sized deer with great ecological plasticity, living under a large diversity of habitats including steppe, boreal and closed temperate forests (Geist, 1999). It is an opportunistic mixed feeder (Hoffmann, 1989), whose diet includes edible portions of trees and shrubs, forbs, grass and sedges (e.g., Gebczynska, 1980; Heptner et al., 1989; Gebert and Verheyden-Tixier, 2001). European red deer tend to favour forbs, foliage and browse, while Siberian and American red deer consume higher proportions of grass (Geist, 1999). In Europe,

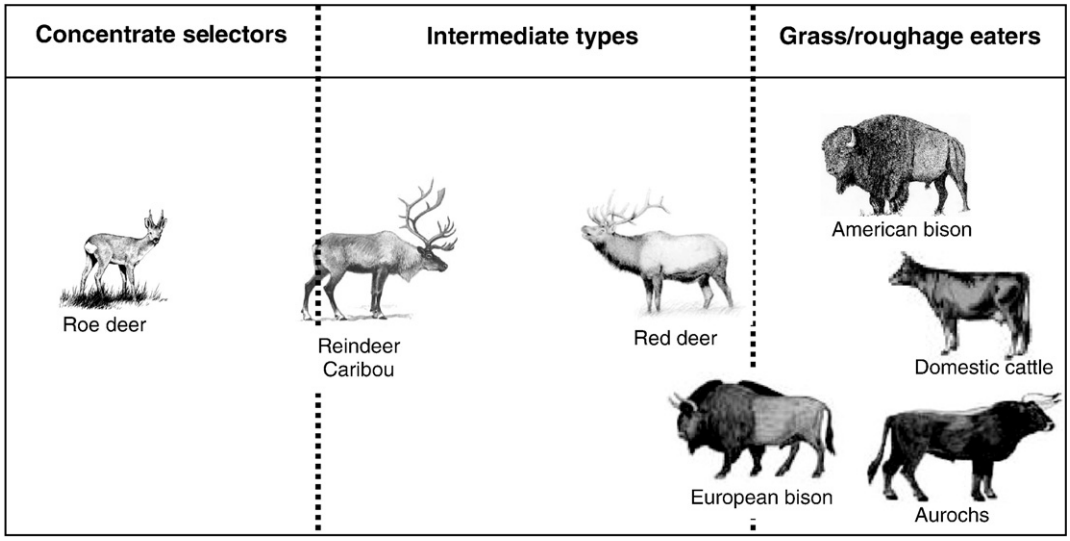

Fig. 1. Dietary classification of the studied species (modified from Hoffmann, 1989; Kie et al., 2003).

most red deer populations live close to areas of human activities, making it very difficult to avoid anthropogenic interference. However, this species was present in many parts of France during the Late Pleistocene and the Holocene without discontinuity.

Roe deer (*Capreolus capreolus*) is a small deer ranging from Europe to Siberia (Geist, 1999). They are specialised concentrate feeders and consume selectively the nutrient-rich parts of plants (Hoffmann, 1989). They may live in a wide variety of habitats, occurring in almost all of the natural habitats found in Europe, including deciduous, coniferous and Mediterranean forests, shrublands, moorlands and marshes. Only high alpine areas and the most open grasslands are rarely occupied (Linnell et al., 1998; Geist, 1999). As for red deer, most European roe deer populations live close to areas of human activities, making it very difficult to avoid anthropogenic interference. This species was present in southern France since the beginning of the Bölling (e.g., Hufthammer and Aaris-Sorensen, 1998) and expanded later in northern areas (Bridault and Chaix, 2002).

The bovini considered here belong to several species: American bison (*Bison bison*), European wisent (*Bison bonasus*), steppe bison (*Bison priscus*) and aurochs (*Bos primigenius*). The last two species, nowadays extinct, are present in the Late-glacial and early Holocene deposits of France. Both modern bison species have narrowly escaped extinction during historical periods and correspond to relic or reintroduced populations. The American bison is found in grassland and woodland habitats in USA and Canada. American bison are grazers that consume essentially graminoids (i.e. grass and sedges) (e.g., Plumb and Dodd, 1993; Coppedege et al., 1998; Fortin et al., 2003). European bison includes some browse in their diet, but a majority of their forage is composed of graminoids (Pucek et al., 2002). Among ruminants, it is classified as a grass/roughage eater (Hoffmann, 1989). The extinct steppe bison *Bison priscus* and the aurochs *Bos primigenius* were both grass eaters with slightly different ecological preferences, drier steppes in the case of steppe bison and more wooded and humid contexts for aurochs (von Koenigswald, 1999).

An additional advantage to choose these species is the possibility to compare carbon isotopic results for specialised feeders, such as roe deer, with those of more generalists, such as red deer and bison, in the same environment. The dietary characteristics of these species are summarized in Fig. 1. It will be therefore possible to compare the carbon isotope variations for species which do not change their diet between open and closed habitats and for species which can change their diet when they change habitat.

3. Materials and methods

To investigate evidence for the canopy effect in high and mid-latitude environments, we used carbon isotopic data from herbivores of modern ecosystems ranging from open tundra to dense temperate forest. We concentrated our efforts on those ecosystems for which a maximum of information was available about the ecology of the animals, especially their diet and the plant formations where they live, and about the carbon isotopic data of animals and the plants they fed on.

Table 1
Description of the modern ecosystems selected to investigate the impact of the canopy effect on carbon-13 abundances in plants and herbivores

Taxon	Material	Location–temperature–precipitation	Environment	References
Reindeer	Collagen	Qamanirjuaq (Nunavut, Canada) 0–200 m asl, 60–64° N, 93–97°W Min temp=−32 °C, max temp=+5 °C Annual prec.<250 mm/year	Arctic tundra	Drucker et al. (2001)
Reindeer	Hair	Queen Maud Gulf (Nunavut, Canada) 200–500 m asl, 60–68° N, 105–120°W Min temp=−32 °C, max temp=+5 °C Annual prec.<250 mm/year	Arctic tundra	This study
Red deer American bison Reindeer	Hair	Central Saskatchewan, Canada 53°63'N, 106°2'W Mean temp=0.4 °C, min temp=−25 °C, max temp=+25 °C Annual prec.=400–500 mm/year	boreal forest, primarily aspen, spruce, pine, poplar	Urton and Hobson, 2005
Reindeer	Collagen	Northeastern Yakutia, 0–200 m, 66°N, 150°E Min temp=−40 °C, max temp=+13 °C Annual prec.=200 mm/year	Open taiga/tundra	Bocherens et al., 1996
Red deer Roe deer	Collagen	Cis-Baikal, Siberia, 400–3000 m asl, 51°–56°N, 102°–110°E Mean temp=−0.7 °C, Min temp=−30 °C, max temp=+25 °C Annual prec.=495 mm/year	boreal forest/steppe transitional zone primarily pines, larches, cedars, spruces, firs with a mixture of poplar, birch, aspen	Weber et al., 2002
Red deer Roe deer European bison	Collagen	Bialowieza Forest, Poland, 147–172 m asl 52°43'N, 23°50'E mean temp=6.8 °C, min temp=−4.7 °C, max temp=+17.8 °C annual prec.= 641 mm/year	temperate deciduous forest zone primarily oak, lime, hornbeam with a mixture of ash, maple and elm	Bocherens and Drucker, 2003, and this work
Roe deer	Collagen	Dourdan Forest, France, 100 m asl 48°19'N, 2°01'E mean temp=11.7 °C, min temp=3 °C, max temp=18.5 °C annual prec.=630 mm/year	temperate deciduous forest, primarily beech	Rodière et al., 1996

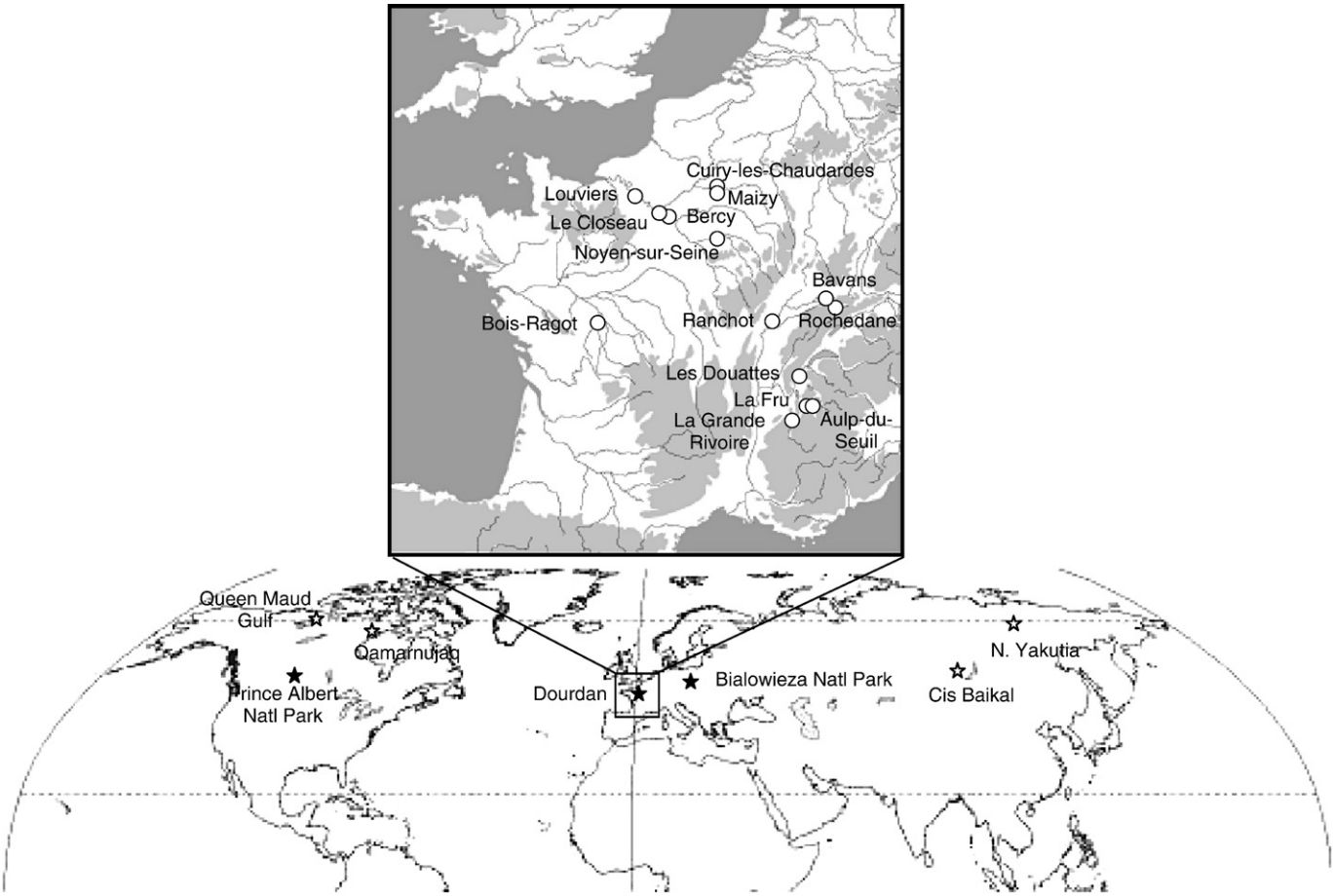

Fig. 2. Map depicting the location of the sites discussed in the text. White stars correspond to modern sites with open environments, black stars correspond to modern sites with closed-canopy environments, white circles correspond to archaeological sites with faunal material documenting the late Glacial to Holocene transition in France.

The selected modern specimens and their origin are described in detail in Table 1 and the location of the sites is shown on Fig. 2. To avoid anthropogenic influences on the isotopic record of the diet as much as possible, our selected large herbivores were free-ranging wild animals. Bone and hair material of modern ruminants comes from seven localities in North America and Eurasia (Table 1; Fig. 2). Caribou and reindeer from open (Queen Maud Gulf, Qamanirjuaq, Northern Yakutia) and closed forested (Central Saskatchewan) environments have been selected. Red deer specimens are from closed forested environments (Central Saskatchewan and Bialowieza Forest National Park) and more open environments (Cis-Baikal). Roe deer specimens are also from closed forested environments (Dourdan forest and Bialowieza Forest National Park) and more open environments (Cis-Baikal). Bison specimens are from closed forest environments (Central Saskatchewan and Bialowieza Forest National Park). Except for Queen Maud Gulf caribou which are unpublished data, all of the isotopic data were previously published in various works (Table 1). In the present paper, they were corrected from variations of $\delta^{13}C$ values in atmospheric CO_2 between 1966 and 2003.

Isotopic data from modern large herbivores were obtained for hair keratin and bone collagen, involving different diet-tissue isotopic discrimination factors, which prevented direct comparison of $\delta^{13}C$ values. Therefore, measured $\delta^{13}C$ values were converted to diet $\delta^{13}C$ values ($\delta^{13}C_{diet}$) using the average fractionation factor between the mean diet and the considered tissue inferred from the literature (Vogel, 1978; van der Merwe, 1989; Ambrose, 1993; Rodière et al., 1996; Sponheimer et al., 2003; Ayliffe et al., 2004) and summarised in Table 2. Moreover, since isotopic analyses were performed on specimens living at different times, we took into account the rapid changes in $\delta^{13}C$ value of atmospheric CO_2 linked to modern industrial activities and deforestation. The $\delta^{13}C_{diet}$ values were thus set to a similar atmospheric $\delta^{13}C$ value of −7‰, the average value during Upper Pleistocene times (Leuenberger et al., 1992) by using a correction formula presented by Feng (1998).

To examine the decline in $\delta^{13}C$ values of different species during the Late-Glacial/Early Holocene transition, we selected ancient bone specimens of cervids, red deer and roe deer, and large bovines, namely wild bovine and domestic cattle, from a restricted geographic area, the Paris Basin. The material comes from seven sites, with chronological

Table 2
Review of ^{13}C discrimination between hair and collagen of modern large herbivores and their diet

Tissue	Taxon	$\Delta\delta^{13}C$ tissue-diet	Reference
Hair	Horse	2.7	Ayliffe et al., 2004
Hair	Cattle	2.7	Sponheimer et al., 2003
Hair	Goat	3.2	Sponheimer et al., 2003
Hair	Alpaca	3.2	Sponheimer et al., 2003
Hair	Llama	3.5	Sponheimer et al., 2003
Hair	Rabbit	3.4	Sponheimer et al., 2003
	MEAN	3.1	
	SD	0.3	
Collagen	Bison	5.0	Ambrose, 1993
Collagen	Giraffe	5.5	Ambrose, 1993
Collagen	C_3 eater herbivores	5.0	van der Merwe, 1989
Collagen	C_3 eater herbivores	5.3	Vogel, 1978a
Collagen	Roe deer	4.5	Rodière et al., 1996
	MEAN	5.1	
	SD	0.3	

Table 3
Isotopic values for large herbivores from modern ecosystems. Data are from Weber et al. (2002) for boreal forest–steppe of Siberia, from Rodière et al. (1996) for temperate forest of Dourdan, and from Urton and Hobson (2005) for boreal forest of western Canada

Species	Lab n°	Site	Habitat	Tissue	Year	$\delta^{13}C$ tissue	$\delta^{13}C$ diet calculated $\delta^{13}C$ coll − 5.1 $\delta^{13}C$ hair − 3.1	$\Delta^{13}C$ atm	$\delta^{13}C$ diet Calculated corrected	Ref.
Reindeer	204	Qamanirjuaq, Nunavut	Arctic tundra	Collagen	1966	−19.4	−24.5	0.24	−24.2	Drucker et al. (2001)
Reindeer	216	Qamanirjuaq, Nunavut	Arctic tundra	Collagen	1966	−19.5	−24.6	0.24	−24.3	Drucker et al. (2001)
Reindeer	692	Qamanirjuaq, Nunavut	Arctic tundra	Collagen	1967	−19.2	−24.3	0.26	−24.0	Drucker et al. (2001)
Reindeer	80	Qamanirjuaq, Nunavut	Arctic tundra	Collagen	1966	−20.0	−25.1	0.24	−24.8	Drucker et al. (2001)
Reindeer	397-1	Qamanirjuaq, Nunavut	Arctic tundra	Collagen	1967	−19.6	−24.7	0.26	−24.4	Drucker et al. (2001)
Reindeer	397-2	Qamanirjuaq, Nunavut	Arctic tundra	Collagen	1967	−18.8	−23.9	0.26	−23.6	Drucker et al. (2001)
Reindeer	22882	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2002	−22.4	−25.5	1.20	−24.3	This work
Reindeer	22883	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2002	−23.0	−26.1	1.20	−24.9	This work
Reindeer	22884	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2002	−22.0	−25.1	1.20	−23.9	This work
Reindeer	22885	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2002	−22.4	−25.5	1.20	−24.3	This work
Reindeer	22886	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2002	−22.6	−25.7	1.20	−24.5	This work
Reindeer	22968	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.9	−26.0	1.23	−24.7	This work
Reindeer	22969	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−23.1	−26.2	1.23	−24.9	This work
Reindeer	22970	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.5	−25.6	1.23	−24.3	This work
Reindeer	22971	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.4	−25.5	1.23	−24.3	This work
Reindeer	22972	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.8	−25.9	1.23	−24.7	This work
Reindeer	22973	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.8	−25.9	1.23	−24.7	This work
Reindeer	22974	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−23.1	−26.2	1.23	−24.9	This work
Reindeer	22975	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.0	−25.1	1.23	−23.9	This work
Reindeer	22976	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.9	−26.0	1.23	−24.8	This work
Reindeer	22977	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.4	−25.5	1.23	−24.2	This work
Reindeer	22978	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−21.9	−25.0	1.23	−23.8	This work
Reindeer	22980	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−23.4	−26.5	1.23	−25.3	This work
Reindeer	22981	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−23.0	−26.1	1.23	−24.9	This work
Reindeer	22982	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.8	−25.9	1.23	−24.6	This work
Reindeer	22983	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.3	−25.4	1.23	−24.1	This work
Reindeer	22984	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−23.0	−26.1	1.23	−24.9	This work
Reindeer	22985	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.2	−25.3	1.23	−24.0	This work
Reindeer	28053	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−22.1	−25.2	1.23	−23.9	This work
Reindeer	28054	Queen Maud Gulf, Nunavut	Arctic tundra	Hair	2003	−21.7	−24.8	1.23	−23.6	This work
Reindeer	22924	Central Saskatchewan	Boreal forest	Hair	1992	−23.4	−26.5	0.85	−25.6	Urton and Hobson (2005)
Reindeer	22925	Central Saskatchewan	Boreal forest	Hair	1992	−23.7	−26.8	0.85	−25.9	Urton and Hobson (2005)
Reindeer	22928	Central Saskatchewan	Boreal forest	Hair	1993	−23.7	−26.8	0.88	−25.9	Urton and Hobson (2005)
Reindeer	22931	Central Saskatchewan	Boreal forest	Hair	1996	−23.6	−26.7	0.98	−25.7	Urton and Hobson (2005)
Reindeer	22936	Central Saskatchewan	Boreal forest	Hair	1994	−23.8	−26.9	0.91	−25.9	Urton and Hobson (2005)
Reindeer	22939	Central Saskatchewan	Boreal forest	Hair	1994	−23.6	−26.7	0.91	−25.8	Urton and Hobson (2005)
Reindeer	22940	Central Saskatchewan	Boreal forest	Hair	1994	−23.3	−26.4	0.91	−25.5	Urton and Hobson (2005)
Reindeer	22943	Central Saskatchewan	Boreal forest	Hair	1994	−23.3	−26.4	0.91	−25.5	Urton and Hobson (2005)
Reindeer	22946	Central Saskatchewan	Boreal forest	Hair	1994	−22.9	−26.0	0.91	−25.1	Urton and Hobson (2005)
Reindeer	22948	Central Saskatchewan	Boreal forest	Hair	1994	−23.8	−26.9	0.91	−26.0	Urton and Hobson (2005)
Reindeer	22949	Central Saskatchewan	Boreal forest	Hair	1995	−23.5	−26.6	0.95	−25.6	Urton and Hobson (2005)
Reindeer	22951	Central Saskatchewan	Boreal forest	Hair	1995	−24.0	−27.1	0.95	−26.1	Urton and Hobson (2005)
Reindeer	22957	Central Saskatchewan	Boreal forest	Hair	1995	−23.3	−26.4	0.95	−25.4	Urton and Hobson (2005)
Reindeer	22958	Central Saskatchewan	Boreal forest	Hair	1995	−22.6	−25.7	0.95	−24.7	Urton and Hobson (2005)
Reindeer	101300	Northeastern Yakutia	Open taiga	Collagen	1994	−19.6	−24.7	0.91	−23.8	Bocherens et al. (1996)
Reindeer	102300	Northeastern Yakutia	Open taiga	Collagen	1994	−20.2	−25.3	0.91	−24.4	Bocherens et al. (1996)
Reindeer	102800	Northeastern Yakutia	Open taiga	Collagen	1994	−19.4	−24.5	0.91	−23.6	Bocherens et al. (1996)
Reindeer	102900	Northeastern Yakutia	Open taiga	Collagen	1994	−20.2	−25.3	0.91	−24.4	Bocherens et al. (1996)
Reindeer	103000	Northeastern Yakutia	Open taiga	Collagen	1994	−19.5	−24.6	0.91	−23.7	Bocherens et al. (1996)
Red deer	17258	Central Saskatchewan	Boreal forest	Hair	2002	−25.0	−28.1	1.20	−26.9	Urton and Hobson (2005)
Red deer	17259	Central Saskatchewan	Boreal forest	Hair	2002	−24.8	−27.9	1.20	−26.7	Urton and Hobson (2005)
Red deer	17903	Central Saskatchewan	Boreal forest	Hair	2002	−26.5	−29.6	1.20	−28.4	Urton and Hobson (2005)
Red deer	17904	Central Saskatchewan	Boreal forest	Hair	2002	−26.3	−29.4	1.20	−28.2	Urton and Hobson (2005)
Red deer	17906	Central Saskatchewan	Boreal forest	Hair	2002	−25.6	−28.7	1.20	−27.5	Urton and Hobson (2005)
Red deer	17907	Central Saskatchewan	Boreal forest	Hair	2002	−26.6	−29.7	1.20	−28.5	Urton and Hobson (2005)
Red deer	19986	Central Saskatchewan	Boreal forest	Hair	2002	−27.1	−30.2	1.20	−29.0	Urton and Hobson (2005)
Red deer	22557	Central Saskatchewan	Boreal forest	Hair	2002	−24.2	−27.3	1.20	−26.1	Urton and Hobson (2005)
Red deer	22558	Central Saskatchewan	Boreal forest	Hair	2002	−24.3	−27.4	1.20	−26.2	Urton and Hobson (2005)
Red deer	93.052	Cis-Baikal	Forest–steppe	Collagen	*2000*	−22.4	−27.5	1.12	−26.4	Weber et al. (2002)
Red deer	93.053	Cis-Baikal	Forest–steppe	Collagen	*2000*	−20.4	−25.5	1.12	−24.4	Weber et al. (2002)
Red deer	93.066	Cis-Baikal	Forest–steppe	Collagen	*2000*	−22.7	−27.8	1.12	−26.7	Weber et al. (2002)
Red deer	93.149	Cis-Baikal	Forest–steppe	Collagen	*2000*	−22.1	−27.2	1.12	−26.1	Weber et al. (2002)
Red deer	BLW700	Bialowieza Forest	Deciduous forest	Collagen	1970	−21.7	−26.8	0.31	−26.5	This work
Red deer	BLW800	Bialowieza Forest	Deciduous forest	Collagen	1970	−24.2	−29.3	0.31	−29.0	This work
Red deer	BLW900	Bialowieza Forest	Deciduous forest	Collagen	1970	−24.1	−29.2	0.31	−28.9	This work
Red deer	BLW1000	Bialowieza Forest	Deciduous forest	Collagen	1970	−23.9	−29.0	0.31	−28.7	This work
Red deer	BLW1100	Bialowieza Forest	Deciduous forest	Collagen	1970	−23.1	−28.2	0.31	−27.9	This work
Red deer	ACT500	Bialowieza Forest	Deciduous forest	Collagen	1994	−24.2	−29.3	0.91	−28.4	This work
Roe deer	93.057	Cis-Baikal	Forest–steppe	Collagen	*2000*	−20.6	−25.7	1.12	−24.6	Weber et al. (2002)
Roe deer	93.058	Cis-Baikal	Forest–steppe	Collagen	*2000*	−20	−25.1	1.12	−24.0	Weber et al. (2002)
Roe deer	93.059	Cis-Baikal	Forest–steppe	Collagen	*2000*	−21.6	−26.7	1.12	−25.6	Weber et al. (2002)

(continued on next page)

Table 3 (*continued*)

Species	Lab n°	Site	Habitat	Tissue	Year	$\delta^{13}C$ tissue	$\delta^{13}C$ diet calculated $\delta^{13}C$ coll − 5.1 $\delta^{13}C$ hair − 3.1	$\Delta^{13}C$ atm	$\delta^{13}C$ diet Calculated corrected	Ref.
Roe deer	93.060	Cis-Baikal	Forest–steppe	Collagen	*2000*	−20.4	−25.5	1.12	−24.4	Weber et al. (2002)
Roe deer	93.061	Cis-Baikal	Forest–steppe	Collagen	*2000*	−20.4	−25.5	1.12	−24.4	Weber et al. (2002)
Roe deer	93.062	Cis-Baikal	Forest–steppe	Collagen	*2000*	−22.9	−28.0	1.12	−26.9	Weber et al. (2002)
Roe deer	1204	Dourdan Forest	Deciduous forest	Collagen	1990	−23.4	−28.5	0.79	−27.7	Rodière et al. (1996)
Roe deer	7200	Dourdan Forest	Deciduous forest	Collagen	1990	−25.6	−30.7	0.79	−29.9	Rodière et al. (1996)
Roe deer	9200	Dourdan Forest	Deciduous forest	Collagen	1990	−24.7	−29.8	0.79	−29.0	Rodière et al. (1996)
Roe deer	10200	Dourdan Forest	Deciduous forest	Collagen	1990	−25.1	−30.2	0.79	−29.4	Rodière et al. (1996)
Roe deer	11200	Dourdan Forest	Deciduous forest	Collagen	1990	−26.0	−31.1	0.79	−30.3	Rodière et al. (1996)
Roe deer	14200	Dourdan Forest	Deciduous forest	Collagen	1990	−23.8	−28.9	0.79	−28.1	Rodière et al. (1996)
Roe deer	15200	Dourdan Forest	Deciduous forest	Collagen	1990	−25.7	−30.8	0.79	−30.0	Rodière et al. (1996)
Roe deer	20200	Dourdan Forest	Deciduous forest	Collagen	1990	−23.8	−28.9	0.79	−28.1	Rodière et al. (1996)
Roe deer	22200	Dourdan Forest	Deciduous forest	Collagen	1990	−26.1	−31.2	0.79	−30.4	Rodière et al. (1996)
Roe deer	23200	Dourdan Forest	Deciduous forest	Collagen	1990	−24.9	−30.0	0.79	−29.2	Rodière et al. (1996)
Roe deer	24200	Dourdan Forest	Deciduous forest	Collagen	1990	−25.7	−30.8	0.79	−30.0	Rodière et al. (1996)
Roe deer	25200	Dourdan Forest	Deciduous forest	Collagen	1990	−24.9	−30.0	0.79	−29.2	Rodière et al. (1996)
Roe deer	26200	Dourdan Forest	Deciduous forest	Collagen	1990	−25.6	−30.7	0.79	−29.9	Rodière et al. (1996)
Roe deer	27200	Dourdan Forest	Deciduous forest	Collagen	1990	−23.5	−28.6	0.79	−27.8	Rodière et al. (1996)
Roe deer	28200	Dourdan Forest	Deciduous forest	Collagen	1990	−24.1	−29.2	0.79	−28.4	Rodière et al. (1996)
Roe deer	29200	Dourdan Forest	Deciduous forest	Collagen	1990	−23.8	−28.9	0.79	−28.1	Rodière et al. (1996)
Roe deer	30200	Dourdan Forest	Deciduous forest	Collagen	1990	−24.9	−30.0	0.79	−29.2	Rodière et al. (1996)
Roe deer	2203	Dourdan Forest	Deciduous forest	Collagen	1990	−23.7	−28.8	0.79	−28.0	Rodière et al. (1996)
Roe deer	BLW1200	Bialowieza Forest	Deciduous forest	Collagen	1969	−23.2	−28.3	0.29	−28.0	Bocherens and Drucker (2003)
Roe deer	BLW1300	Bialowieza Forest	Deciduous forest	Collagen	1970	−24.5	−29.6	0.31	−29.3	Bocherens and Drucker (2003)
Roe deer	BLW1400	Bialowieza Forest	Deciduous forest	Collagen	1994	−23.5	−28.6	0.91	−27.7	Bocherens and Drucker (2003)
Roe deer	BLW1500	Bialowieza Forest	Deciduous forest	Collagen	1994	−24.0	−29.1	0.91	−28.2	Bocherens and Drucker (2003)
Roe deer	BLW1600	Bialowieza Forest	Deciduous forest	Collagen	1995	−24.8	−29.9	0.95	−29.0	Bocherens and Drucker (2003)
Bison	17270	Central Saskatchewan	Boreal forest	Hair	2002	−25.1	−28.2	1.20	−27.0	Urton and Hobson (2005)
Bison	17271	Central Saskatchewan	Boreal forest	Hair	2002	−23.5	−26.6	1.20	−25.4	Urton and Hobson (2005)
Bison	17272	Central Saskatchewan	Boreal forest	Hair	2002	−24.7	−27.8	1.20	−26.6	Urton and Hobson (2005)
Bison	19969	Central Saskatchewan	Boreal forest	Hair	2002	−25.4	−28.5	1.20	−27.3	Urton and Hobson (2005)
Bison	19970	Central Saskatchewan	Boreal forest	Hair	2002	−26.3	−29.4	1.20	−28.2	Urton and Hobson (2005)
Bison	19972	Central Saskatchewan	Boreal forest	Hair	2002	−26.6	−29.7	1.20	−28.5	Urton and Hobson (2005)
Bison	19973	Central Saskatchewan	Boreal forest	Hair	2002	−25.7	−28.8	1.20	−27.6	Urton and Hobson (2005)
Bison	19974	Central Saskatchewan	Boreal forest	Hair	2002	−25.9	−29.0	1.20	−27.8	Urton and Hobson (2005)
Bison	19975	Central Saskatchewan	Boreal forest	Hair	2002	−25.9	−29.0	1.20	−27.8	Urton and Hobson (2005)
Bison	BLW100	Bialowieza Forest	Deciduous forest	Collagen	1987	−23.2	−28.3	0.71	−27.6	Bocherens and Drucker (2003)
Bison	BLW300	Bialowieza Forest	Deciduous forest	Collagen	1998	−23.0	−28.1	1.05	−27.1	Bocherens and Drucker (2003)
Bison	BLW400	Bialowieza Forest	Deciduous forest	Collagen	1998	−23.7	−28.8	1.05	−27.8	Bocherens and Drucker (2003)
Bison	BLW500	Bialowieza Forest	Deciduous forest	Collagen	1999	−24.4	−29.5	1.08	−28.4	Bocherens and Drucker (2003)
Bison	BLW600	Bialowieza Forest	Deciduous forest	Collagen	1999	−25.6	−30.7	1.08	−29.6	Bocherens and Drucker (2003)
Bison	ACT400	Bialowieza Forest	Deciduous forest	Collagen	1994	−23.6	−28.7	0.91	−27.8	Bocherens and Drucker (2003)

Tissue $\delta^{13}C$ values correspond to those measured on a given tissue; calculated $\delta^{13}C_{diet}$ corresponds to the $\delta^{13}C$ values of the mean diet of the herbivore inferred from the mean $\Delta\delta^{13}C$ tissue-diet calculated in Table 2. $\Delta^{13}C$ atm stands for the difference in the atmospheric CO_2 $\delta^{13}C$ value between the date of the sampling and the Upper Pleistocene time (−7‰ in average). Corrected $\delta^{13}C_{diet}$ values correspond to the $\delta^{13}C_{diet}$ values set to the same atmospheric CO_2 $\delta^{13}C$ value of −7‰.

attributions based on archaeological descriptions presented in the original works. In this paper, the term wild bovine refers to bison (*Bison* sp.) and aurochs (*Bos primigenius*). When the species was specifically identified by osteological analysis, bison and aurochs provided the same collagen $\delta^{13}C$ values (Bocherens et al., 2005a,b; and unpublished data). The acquired isotopic data were augmented with data from Bocherens et al. (2005a,b) for the site of Louviers, and from Balasse (1999) for the sites of Cuiry-les-Chaudardes and Maizy. To consider $\delta^{13}C$ trends through time, we adopted the classical chronological subdivision of Late-Glacial/Early Holocene into chronozones (see Mangerud et al., 1974).

Potential regional effects on herbivore $\delta^{13}C$ values were examined using samples of red deer from threes sites in the Jura and four sites in the northern Alps. Both regions, although geographically close, exhibit differences in faunal succession during the Late-Glacial/Early Holocene transition (Bridault and Chaix, 2002). AMS radiocarbon dating was performed at the Radiocarbon Laboratory of the University of Groningen (The Netherlands) on each sample of collagen red deer, which allowed us to organise our results chronologically. The radiocarbon dates have been calibrated to cal years BP using the IntCal04 calibration dataset (Reimer et al., 2004) with the software calib.5.0.1.

Isotopic data from modern caribou from Queen Maud Gulf were measured on hair, after a cleaning protocol following Urton and Hobson (2005). Isotopic data from all ancient mammals were performed on skeletal collagen. Collagen extraction on modern and ancient material was performed following Bocherens et al. (1997). The reliability of the isotope values were checked using the carbon and nitrogen elemental composition of the collagen (C_{coll}, N_{coll}). Indeed, isotopically well-preserved collagen exhibit C/N_{coll} ratios ranging from 2.9 to 3.6 and percentage of C_{coll} and N_{coll} higher than 8% and 3%, respectively (Ambrose, 1990). Elemental composition of the extracted collagen was measured on a CHN-elemental analyzer (Carlo-Erba NA15000 and Eurovector) coupled to a VG-Optima continuous-flow ratio mass spectrometer used for $^{13}C/^{12}C$ measurements at the Earth Science Department of University P. et M. Curie (Paris, France) and in the Institut des Sciences de l'Evolution (Université Montpellier 2, France). Stable isotope ratios are expressed as $\delta^{13}C$ values relative to the international standard VPDB, with an analytical error of 0.1‰.

4. Results

Values of $\delta^{13}C_{diet}$ calculated from modern large herbivores varied between −30.4‰ to −23.6‰ with an inter-individual variation within a given population that does not exceed 3.1‰, as measured on bison from Central Saskatchewan (Table 3; Fig. 3). Reindeer from Canadian arctic tundra and Siberian open taiga provided some of the highest

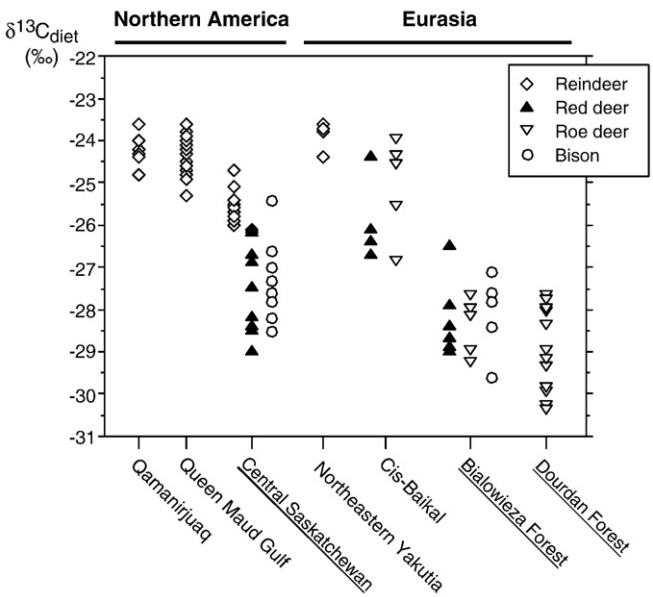

Fig. 3. Review of $\delta^{13}C_{diet}$ values of herbivores from modern ecosystems from North America and Eurasia. Closed-canopy environments are underlined.

$\delta^{13}C_{diet}$ values, while roe deer from temperate forests in Europe exhibited some of the lowest $\delta^{13}C_{diet}$ values.

For a given species, the populations dwelling in a closed canopy forest always exhibited significantly lower $\delta^{13}C$ values than populations dwelling in a more open environment. This is observed when comparing woodland caribou on one hand with barren-ground caribou and open taiga reindeer on the other hand, red deer from boreal or temperate closed canopy forests with red deer from open forest–steppe, roe deer from temperate closed canopy forests with roe deer from steppe and forest–steppe (Fig. 3; Table 4). In contrast, when dealing with a similar type of habitat, open or closed, no significant difference is observed despite clear differences in the geographical origin, the climatic conditions, and the floristic composition. For instance, roe deer from the temperate forest from Dourdan, dominated by beech and roe deer from Bialowieza forest, dominated by oak, lime and hornbeam, exhibit equivalent $\delta^{13}C$ values despite a difference of 6 °C between the average annual temperatures in both locations (Table 1). Moreover, the $\delta^{13}C$ values of a given taxon in closed canopy forest of boreal or temperate type are not significantly different, as for bison and red deer from Central Saskatchewan and Bialowieza Forest (Fig. 3; Table 4). In open environments, barren-ground caribou from both Canadian populations and open taiga reindeer from Yakutia also exhibit equivalent $\delta^{13}C$ values (Table 4). These results are not affected by the tissue used to calculate the $\delta^{13}C$ value of the diet, as well illustrated by barren-ground caribou from Queen Maud Gulf or Qamanirjuaq herds, which provided equivalent $\delta^{13}C_{diet}$ although hair or collagen were sampled.

During the Late-Glacial/Early Holocene transition, the $\delta^{13}C_{diet}$ values of cervids and large bovines from Paris Basin exhibited a significant decrease (Table 5; Fig. 4); however, this decrease differed among species. Indeed, depletion of $\delta^{13}C_{diet}$ values through the transition was more pronounced for wild bovine (−3.3‰) than for red deer (−2.2‰) and roe deer (−2.7‰). As a result, $\delta^{13}C_{diet}$ values of wild bovine were comparable to those of red deer and roe deer during the Boreal/early Atlantic transition (ca. 9100–8000 years cal BP), whereas they were significantly higher (Mann–Whitney *U*-test, $U=21.0$, $p<0.005$) during the Bölling time (ca. 14,700–13,900 years cal BP). The $\delta^{13}C_{diet}$ values of roe deer reached a minimum during the early Atlantic (ca. 9000–7000 years cal BP) after which a small increase was observed. The $\delta^{13}C_{diet}$ values of red deer and wild bovine changed slightly at the end of the Atlantic, towards less depleted values for red deer and more depleted values for wild bovine. Domestic cattle present similar $\delta^{13}C_{diet}$ values as wild bovine during the early Atlantic. In the late Atlantic, the $\delta^{13}C_{diet}$ values of domestic cattle changed towards significantly less-depleted values than wild bovine (Mann–Whitney *U*-test, $p<0.0001$, $U=4.0$, $n>10$).

Dated specimens of red deer from Jura and northern Alps exhibited a general trend of decreasing $\delta^{13}C_{diet}$ values over the Late-Glacial/Early Holocene transition (Tables 6 and 7; Fig. 5). Red deer $\delta^{13}C_{diet}$ values ranged between −24‰ and −27‰ during the Bölling/Alleröd period for both Jura and northern Alps areas. After the Younger Dryas, red deer $\delta^{13}C_{diet}$ values ranged from −27‰ to −29.1‰ in the Jura, while red deer from the northern Alps had $\delta^{13}C_{diet}$ values similar to those observed before the Younger Dryas. As a result, the Late-Glacial/Early Holocene trend in red deer towards about 3‰ lower $\delta^{13}C_{diet}$ values is evidenced in the Jura, but not in the northern Alps. This confirms that, in addition to global change, local factors can account for changes in $\delta^{13}C_{diet}$ of large herbivores at the Early Holocene.

5. Discussion

5.1. Modern ecosystems

For every species considered, the populations dwelling under closed canopy habitats exhibit significantly lower $\delta^{13}C$ values than those dwelling under more open conditions. This was not simply linked to shift from grazing to browsing with increasing forest cover, since it occurred for a specialist feeder like roe deer as well as for a generalist one like red deer. This was not surprising since vascular plants show depleted ^{13}C abundances under closed canopy cover compared to more open conditions. A good illustration of this is the comparison of $\delta^{13}C$ values from Brooks et al. (1997) for boreal forest

Table 4
Statistical comparisons (Mann–Whitney) of $\delta^{13}C$ values obtained on populations from a given species

Taxon	Tissue	Environments (n)	Type	Statistical comparison
Rangifer tarandus	C/H	Qamanirjuaq (arctic tundra) ($n=6$) / Queen Maud Gulf (arctic tundra) ($n=24$)	O/O	$p=0.32$, $U=53.0$
Rangifer tarandus	C/C	Qamanirjuaq (arctic tundra) ($n=6$) / NE Yakutia (open taiga) ($n=5$)	O/O	$p=0.52$, $U=11.5$
Rangifer tarandus	H/C	Queen Maud Gulf (arctic tundra) ($n=24$) / NE Yakutia (open taiga) ($n=5$)	O/O	$p=0.13$, $U=38.5$
Cervus elaphus	H/C	Prince Albert Natl. Park (boreal forest) ($n=9$) / Bialowieza Natl. Park (temperate forest) ($n=6$)	C/C	$p=0.19$, $U=16.0$
Capreolus capreolus	C/C	Dourdan forest (temperate forest) ($n=18$) / Bialowieza Natl. Park (temperate forest) ($n=5$)	C/C	$p=0.19$, $U=27.5$
Bison sp.	H/C	Prince Albert Natl. Park (boreal forest) ($n=9$) / Bialowieza Natl. Park (temperate forest) ($n=6$)	C/C	$p=0.26$, $U=17.5$
Rangifer tarandus	C+H/H	Qamanirjuaq+Queen Maud Gulf (arctic tundra) ($n=30$) / Prince Albert Natl. Park (boreal forest) ($n=14$)	O/C	**$p<0.0001$, $U=10.5$**
Rangifer tarandus	H/H	Queen Maud Gulf (arctic tundra) ($n=24$) / Prince Albert Natl. Park (boreal forest) ($n=14$)	O/C	**$P<0.0001$, $U=9.5$**
Cervus elaphus	C/C	Cis-Baikal (forest–steppe) ($n=6$) / Bialowieza Natl. Park (temperate forest) ($n=6$)	O/C	**$p=0.02$, $U=1.0$**
Cervus elaphus	C/H	Cis-Baikal (forest–steppe) ($n=6$) / Prince Albert Natl. Park (boreal forest) ($n=9$)	O/C	**$p=0.02$, $U=6.0$**
Capreolus capreolus	C/C	Cis-Baikal (forest–steppe) ($n=6$) / Dourdan forest+Bialowieza Natl. Park (temperate forest) ($n=23$)	O/C	**$p=0.0002$, $U=0.0$**

Statistically significant results are shown in bold.
C and H correspond to collagen and hair. O and C correspond to open and closed-canopy environments.

Table 5
Isotopic results for ancient large herbivores from the Paris Basin. Data are from Bocherens et al. (2005a,b) for Louviers site and from Balasse (1999) for Cuiry-les-Chaudardes and Maizy sites

Species	Lab n°	Site	Sample	Excavation n°	Chronozone	Ccoll (%)	Ncoll (%)	C/Ncoll	$\delta^{13}C_{coll}$ (‰)	$\delta^{13}C_{diet}$ (‰)
Red deer	BRG2800	Bois-Ragot (layer 5)	Left tibia	BR 5 I5 736	Bölling	24.6	8.7	3.3	−20.8	−25.9
Red deer	BRG2900	Bois-Ragot (layer 5)	Right radius	BR 5 I1 434	Bölling	19.5	7.7	2.9	−20.0	−25.1
Red deer	BRG3000	Bois-Ragot (layer 5)	Left humerus	BR 5 H2 1096	Bölling	21.5	7.4	3.4	−21.0	−26.1
Red deer	BRG4200	Bois-Ragot (layer 4)	Left scapula	BR 4 I7 252	Bölling	33.2	12.3	3.1	−20.6	−25.7
Red deer	BRG4300	Bois-Ragot (layer 4)	Left scapula	BR 4 J1 67	Bölling	30.1	11.4	3.1	−21.0	−26.1
Red deer	BRG4400	Bois-Ragot (layer 4)	Right metacarpal	BR 4 H2 249	Bölling	36.8	13.3	3.2	−19.7	−24.8
Red deer	BRG4500	Bois-Ragot (layer 4)	Right metacarpal	BR 4 H6 1	Bölling	30.9	12.0	3.0	−20.5	−25.6
Red deer	BRG4600	Bois-Ragot (layer 4)	Right metatarsal	BR 4 H2 163	Bölling	37.5	13.8	3.2	−20.4	−25.5
Red deer	BRG4700	Bois-Ragot (layer 4)	Right metatarsal	BR 4 J7 68	Bölling	32.4	12.3	3.1	−20.1	−25.2
Red deer	BRG4800	Bois-Ragot (layer 4)	Right metatarsal	BR 4 I1 195	Bölling	24.9	9.7	3.0	−21.3	−26.4
Red deer	BRG5900	Bois-Ragot (layer 3)	Metatarsal	BR 3 J3	Bölling	35.4	12.8	3.2	−20.9	−26.0
Red deer	BRG6000	Bois-Ragot (layer 3)	Radius	BR 3 H7-7	Bölling	38.8	14.7	3.1	−20.3	−25.4
Red deer	CLS1000	Le Closeau (locus 46)	Left tibia	LC97IFP3S6L46 E268 139	Bölling	38.0	13.8	3.2	−20.1	−25.2
Red deer	CLS1100	Le Closeau (locus 46)	Left tibia	LC97IFP3S6L46 E270 67	Bölling	35.4	12.8	3.2	−20.2	−25.3
Red deer	CLS1200–3	Le Closeau (locus 46)	Left tibia	LC97IFP3S6L46 D268 280	Bölling	40.5	14.7	3.2	−20.4	−25.5
Red deer	CLS1300	Le Closeau (locus 46)	Right tibia	LC97IFP3S6L46 E267 13	Bölling	38.1	13.9	3.2	−20.5	−25.6
Red deer	CLS1400–1	Le Closeau (locus 46)	Right tibia	LC97IFP3S6L46 D267 82	Bölling	39.1	14.3	3.2	−20.2	−25.3
Red deer	CLS1500	Le Closeau (locus 46)	Right tibia	LC97IFP3S6L46 Z266 15	Bölling	39.1	14.2	3.2	−20.5	−25.6
Red deer	NO100	Noyen-sur-Seine (layer 9)	Right radius	84 XVI C150-8	Boreal/Atlantic	41.6	15.1	3.2	−22.8	−27.9
Red deer	NO300	Noyen-sur-Seine (layer 7d)	Left humerus	84 XV Z153-7	Boreal/Atlantic	39.7	14.2	3.3	−22.7	−27.8
Red deer	NO400	Noyen-sur-Seine (layer 9)	Left humerus	84 XVI H140-6	Boreal/Atlantic	42.0	15.8	3.0	−22.3	−27.4
Red deer	NO600	Noyen-sur-Seine (layer 9)	Left radius	84 XVI D144-6	Boreal/Atlantic	41.6	14.8	3.3	−23.1	−28.2
Red deer	NO4800	Noyen-sur-Seine (layer 9)	Left metacapal	84 XVI E137-12	Boreal/Atlantic	41.8	15.1	3.2	−22.5	−27.6
Red deer	NO5000	Noyen-sur-Seine (layer 9)	Left metacapal	84 XVI D143-15	Boreal/Atlantic	42.5	15.6	3.2	−22.5	−27.6
Red deer	CCF cer 1	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	40.2	14.7	3.2	−22.8	−27.9
Red deer	CCF cer 2	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	39.9	14.6	3.2	−22.7	−27.8
Red deer	CCF cer 3	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	39.3	14.4	3.2	−23.4	−28.5
Red deer	CCF cer 4	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	32.4	11.8	3.2	−20.6	−25.7
Red deer	CCF cer 5	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	41.3	15.2	3.2	−24.0	−29.1
Red deer	MGA cer 1	Maizy	n.g.	n.g.	Late Atlantic	40.5	14.8	3.2	−20.2	−25.3
Red deer	MGA cer 2	Maizy	n.g.	n.g.	Late Atlantic	41.8	15.4	3.2	−22.7	−27.8
Red deer	MGA cer 3	Maizy	n.g.	n.g.	Late Atlantic	36.9	13.5	3.2	−22.2	−27.3
Red deer	MGA cer 4	Maizy	n.g.	n.g.	Late Atlantic	40.8	15.0	3.2	−22.9	−28.0
Red deer	B2601	Bercy	Humerus	QS, L XVI,25 c21	Late Atlantic	39.4	13.3	3.5	−23.0	−28.1
Red deer	B5000	Bercy	Radius	QS, M XV,8 c2	Late Atlantic	39.5	14.6	3.2	−23.3	−28.4
Red deer	B5400	Bercy	Metapodal	QS, M XV,11	Late Atlantic	39.7	14.6	3.2	−21.6	−26.7
Red deer	B5200	Bercy	Radius	QS, M XV,14 c2	Late Atlantic	40.9	15.0	3.2	−23.5	−28.6
Red deer	B5100	Bercy	Radius	QS, M XV,20 c2n3	Late Atlantic	42.1	15.4	3.2	−22.3	−27.4
Red deer	B5300	Bercy	Humerus	QS, M XV,20 c2n4	Late Atlantic	37.5	13.7	3.2	−22.5	−27.6
Red deer	B4800	Bercy	Tibia	QS, M XV,14 c2n4	Late Atlantic	41.5	15.2	3.2	−21.4	−26.5
Red deer	Lo3000	Louviers	Left humerus	A c18 24,84	Late Atlantic	44.2	15.1	3.4	−22.0	−27.1
Red deer	Lo3100	Louviers	Right radius	A c18 24,83	Late Atlantic	44.7	15.5	3.4	−22.4	−27.5
Red deer	Lo3200	Louviers	Right radius	A c18 24,82	Late Atlantic	44.5	15.4	3.4	−22.1	−27.2
Red deer	Lo3300	Louviers	Left humerus	A c16 29,92	Late Atlantic	44.7	15.2	3.4	−22.2	−27.3
Red deer	Lo3400	Louviers	Right tibia	A c16 34,80	Late Atlantic	44.1	14.8	3.5	−22.9	−28.0
Roe deer	BRG700	Bois-Ragot (layer 6)	Metatarsal	BR 6 G4 559	Bölling	35.6	13.3	3.1	−20.2	−25.3
Roe deer	BRG800	Bois-Ragot (layer 6)	Femur	BR 6 G4 508	Bölling	28.1	11.2	2.9	−20.9	−26.0
Roe deer	BRG5000	Bois-Ragot (layer 4)	Metatarsal	BR 4 J2 173	Bölling	36.8	13.9	3.1	−20.4	−25.5
Roe deer	BRG5100	Bois-Ragot (layer 4)	Metatarsal	BR 4 K5 79	Bölling	18.1	6.9	3.1	−19.0	−24.1
Roe deer	BRG6300	Bois-Ragot (layer 3)	Metacarpal	BR 3 J5-110	Bölling	39.2	14.9	3.1	−20.5	−25.6
Roe deer	BRG6400	Bois-Ragot (layer 3)	Metacarpal	BR 3 H1-26	Bölling	37.4	13.9	3.1	−20.9	−26.0
Roe deer	NO2100	Noyen-sur-Seine (layer 9)	Phalanx I	83 XVI E140	Boreal/Atlantic	42.0	15.5	3.2	−22.7	−27.8
Roe deer	NO2200	Noyen-sur-Seine (layer 9)	Phalanx I	83 XVI E140	Boreal/Atlantic	42.3	15.5	3.2	−22.4	−27.5
Roe deer	NO2400	Noyen-sur-Seine (layer 9)	Phalanx I	84 XVI Y151-36	Boreal/Atlantic	41.9	15.2	3.3	−23.1	−28.2
Roe deer	NO5300	Noyen-sur-Seine (layer 9)	Left femur	84 XV Z151-36	Boreal/Atlantic	41.6	15.1	3.2	−22.9	−28.0
Roe deer	NO5400	Noyen-sur-Seine (layer 9)	Left tibia	84 XVI G142-6	Boreal/Atlantic	42.2	15.5	3.2	−22.8	−27.9
Roe deer	NO5600	Noyen-sur-Seine (layer 9)	Phalanx I	84 XVI H132-38	Boreal/Atlantic	42.7	15.7	3.2	−23.2	−28.3
Roe deer	NO5500	Noyen-sur-Seine (layer 9)	Left tibia	84 XVI E141-2	Boreal/Atlantic	42.8	15.8	3.2	−23.8	−28.9
Roe deer	CCF ch 1	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	39.6	14.4	3.2	−23.4	−28.5
Roe deer	CCF ch 2	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	41.4	15.1	3.2	−23.7	−28.8
Roe deer	CCF ch 3	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	39.8	14.6	3.2	−22.8	−27.9
Roe deer	CCF ch 4	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	41.5	15.2	3.2	−24.5	−29.6
Roe deer	CCF ch 5	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	40.4	14.7	3.2	−24.4	−29.5
Roe deer	Lo4700	Louviers	Skull	c12 42,83	Late Atlantic	40.9	13.6	3.5	−23.9	−29.0
Roe deer	B4200	Bercy	Jawbone	QS, N XIII,13 c,15 st,37	Late Atlantic	38.4	13.7	3.3	−22.3	−27.4
Roe deer	B4300	Bercy	Scapula	QS, M XX,11 c,21	Late Atlantic	39.7	14.3	3.2	−22.2	−27.3
Roe deer	B4400	Bercy	Scapula	QS, M XV,15 c,2n3	Late Atlantic	41.2	15.2	3.2	−23.2	−28.3
Roe deer	B4500	Bercy	Radius and ulna	QS, M XV,14	Late Atlantic	41.1	15.1	3.2	−22.8	−27.9
Wild bovine	BRG1400	Bois-Ragot (layer 6)	Inf M3	BR 6 H4 242	Bölling	41.8	15.3	3.2	−19.5	−24.6
Wild bovine	BRG3100	Bois-Ragot (layer 5)	Humerus G	BR 5 J4 819	Bölling	41.0	15.2	3.2	−19.5	−24.6
Wild bovine	BRG3200	Bois-Ragot (layer 5)	Humerus G	BR 5 F2 147	Bölling	39.2	15.0	3.1	−19.9	−25.0
Wild bovine	BRG3700	Bois-Ragot (layer 4)	Radius D	BR 4 I5 608	Bölling	39.0	14.8	3.1	−19.4	−24.5
Wild bovine	BRG3800	Bois-Ragot (layer 4)	Radius D	BR 4 J4 706	Bölling	35.5	13.8	3.0	−19.8	−24.9

Table 5 (*continued*)

Species	Lab n°	Site	Sample	Excavation n°	Chronozone	Ccoll (%)	Ncoll (%)	C/Ncoll	$\delta^{13}C_{coll}$ (‰)	$\delta^{13}C_{diet}$ (‰)
Wild bovine	BRG3900	Bois-Ragot (layer 4)	Phalanx I	BR 4 J4 591	Bölling	34.9	13.3	3.1	−20.0	−25.1
Wild bovine	BRG4000	Bois-Ragot (layer 4)	Humerus	BR 4 J3 565	Bölling	35.3	13.6	3.0	−19.1	−24.2
Wild bovine	BRG4100	Bois-Ragot (layer 4)	Humerus	BR 4 J3 677	Bölling	35.5	13.5	3.1	−20.4	−25.5
Wild bovine	NO1600	Noyen-sur-Seine (layer 9)	Phalanx III	84 XVI C150-8	Boreal/Atlantic	41.4	14.8	3.3	−23.5	−28.6
Wild bovine	NO1900	Noyen-sur-Seine (layer 9)	Metapodal	84 XVI C149-6	Boreal/Atlantic	41.7	15.2	3.2	−23.4	−28.5
Wild bovine	NO2000	Noyen-sur-Seine (layer 9)	Metatarsal	84 XV TZ153-9	Boreal/Atlantic	41.5	15.1	3.2	−22.8	−27.9
Wild bovine	NO5100	Noyen-sur-Seine (layer 9)	Left metatarsal	84 XVI G144-4	Boreal/Atlantic	42.5	15.4	3.2	−22.9	−28.0
Wild bovine	NO5200	Noyen-sur-Seine (layer 9)	Left tibia	84 XVI B148-14	Boreal/Atlantic	41.7	15.2	3.2	−22.6	−27.7
Wild bovine	CCF aur 1	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	32.0	11.6	3.2	−22.6	−27.7
Wild bovine	CCF aur 2	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	31.1	11.4	3.2	−23.0	−28.1
Wild bovine	CCF aur 3	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	28.1	10.3	3.2	−23.5	−28.6
Wild bovine	CCF aur 4	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	37.0	13.6	3.2	−23.6	−28.7
Wild bovine	CCF aur 5	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	42.5	15.6	3.2	−23.5	−28.6
Wild bovine	CCF aur 6	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	41.1	15.1	3.2	−22.7	−27.8
Wild bovine	MGA aur 1	Maizy	n.g.	n.g.	Late Atlantic	40.3	14.8	3.2	−24.0	−29.1
Wild bovine	MGA aur 2	Maizy	n.g.	n.g.	Late Atlantic	42.4	15.5	3.2	−23.8	−28.9
Wild bovine	MGA aur 3	Maizy	n.g.	n.g.	Late Atlantic	36.9	13.6	3.2	−24.5	−29.6
Wild bovine	B2001	Bercy	Radius	QS, L XV, 15 c21	Late Atlantic	38.3	12.9	3.5	−23.6	−28.7
Wild bovine	B2201C	Bercy	Tibia	QS, L XII,13 c21	Late Atlantic	43.0	15.4	3.3	−24.0	−29.1
Wild bovine	B5500	Bercy	Sacrum	QS, M XV,8 c2n4	Late Atlantic	41.7	15.3	3.2	−23.4	−28.5
Wild bovine	B5600C	Bercy	Metatarsal	QS, L XV,24 c21	Late Atlantic	42.5	15.3	3.2	−23.4	−28.5
Wild bovine	B6100C	Bercy	Humerus	QS, L XV,12 c21	Late Atlantic	42.5	15.3	3.2	−23.7	−28.8
Wild bovine	B6200C	Bercy	Radius and ulna	QS, K XVIII,25 c21	Late Atlantic	43.5	15.7	3.2	−23.1	−28.2
Wild bovine	Lo3600	Louviers	Phalanx I	A c18 34,80	Late Atlantic	44.2	15.3	3.4	−23.6	−28.7
Wild bovine	Lo3700	Louviers	Phalanx I	A c18 48,81	Late Atlantic	43.8	15.1	3.4	−22.8	−27.9
Wild bovine	Lo3900	Louviers	Humerus	A c18 53,80	Late Atlantic	43.8	15.0	3.4	−23.0	−28.1
Wild bovine	Lo4000	Louviers	Right metacarpal	A c16 31,82	Late Atlantic	43.9	15.1	3.4	−22.7	−27.8
Cattle	CCF303	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	41.8	15.2	3.2	−23.2	−28.3
Cattle	CCF502	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	42.7	15.5	3.2	−23.5	−28.6
Cattle	CCF803	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	42.6	15.7	3.2	−22.8	−27.9
Cattle	CCF1302	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	42.2	15.4	3.2	−22.2	−27.3
Cattle	CCF1403	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	41.0	14.9	3.2	−23.0	−28.1
Cattle	CCF1503	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	41.5	15.1	3.2	−22.5	−27.6
Cattle	CCF1603	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	40.1	14.8	3.2	−23.5	−28.6
Cattle	CCF1701	Cuiry-les-Chaudardes	n.g.	n.g.	Early Atlantic	40.6	14.9	3.2	−23.4	−28.5
Cattle	MGA300	Maizy	n.g.	n.g.	Late Atlantic	42.7	15.6	3.2	−22.3	−27.4
Cattle	MGA500	Maizy	n.g.	n.g.	Late Atlantic	40.9	15.1	3.2	−22.2	−27.3
Cattle	MGA603	Maizy	n.g.	n.g.	Late Atlantic	42.9	15.7	3.2	−21.9	−27.0
Cattle	MGA703	Maizy	n.g.	n.g.	Late Atlantic	30.2	10.8	3.3	−21.6	−26.7
Cattle	B8600	Bercy	Metapodal	QS, M XV,10 c2n4	Late Atlantic	41.5	15.3	3.2	−21.6	−26.7
Cattle	B8500	Bercy	Tibia	QS, M XV,14 c2n4	Late Atlantic	40.9	15.0	3.2	−22.7	−27.8
Cattle	B7400	Bercy	Radius	QS, M XVI,22 c22	Late Atlantic	40.3	14.9	3.2	−21.3	−26.4
Cattle	B7500	Bercy	Radius	QS, M XVI,22 c21	Late Atlantic	40.1	14.8	3.2	−21.9	−27.0
Cattle	B8700	Bercy	Metapodal	QS, M XV,8 c2n4	Late Atlantic	41.8	15.4	3.2	−22.0	−27.1
Cattle	B8800	Bercy	Metapodal	QS, M XV,18 c2n4	Late Atlantic	41.6	14.9	3.3	−21.8	−26.9
Cattle	B8900	Bercy	Tibia	QS, M XVI,3 c1	Late Atlantic	41.6	14.8	3.3	−21.8	−26.9
Cattle	Lo200	Louviers	Right humerus	A c12 29,85	Late Atlantic	44.5	15.2	3.4	−21.8	−26.9
Cattle	Lo700	Louviers	Left radius	A c12 54,84	Late Atlantic	43.6	14.8	3.4	−22.5	−27.6
Cattle	Lo1300	Louviers	Left tibia	A c12 35,81	Late Atlantic	45.2	15.1	3.5	−22.6	−27.7
Cattle	Lo1400	Louviers	Right radius	A c12 30,83	Late Atlantic	46.2	15.8	3.4	−22.1	−27.2
Cattle	Lo1600	Louviers	Right radius	A c18 57,79	Late Atlantic	43.0	14.9	3.4	−23.1	−28.2
Cattle	Lo1700	Louviers	Right radius	A c18 22,77	Late Atlantic	44.5	14.9	3.5	−21.2	−26.3
Cattle	Lo1900	Louviers	Left radius	A c18 62,77	Late Atlantic	44.5	14.8	3.5	−22.4	−27.5
Cattle	Lo2000	Louviers	Right tibia	A c18 53,80	Late Atlantic	44.4	14.7	3.5	−21.8	−26.9
Cattle	Lo2100	Louviers	Right tibia	A c18 42,77	Late Atlantic	44.5	15.2	3.4	−22.3	−27.4

Tissue $\delta^{13}C_{coll}$ values correspond to $\delta^{13}C$ values measured on skeletal collagen; $\delta^{13}C_{diet}$ values correspond to the $\delta^{13}C_{coll}$ values −5.1‰. n.g. stands for not given.

compared to those from Barnett (1994) for arctic tundra (Fig. 6). Vascular plants do not exhibit significant differences in their $\delta^{13}C$ values in closed canopy conditions (e.g., Gebauer and Meyer, 2003). It is therefore not surprising to find no difference in the $\delta^{13}C$ values of ruminants dwelling under closed canopy forest, even with different dietary preferences. Only lichens exhibit systematically more positive $\delta^{13}C$ values than coeval vascular plants (e.g., Fizet et al., 1995; Heaton, 1999; Jahren et al., 2003). Indeed, reindeer, which consume high amounts of lichen, had more positive $\delta^{13}C$ values than coeval ruminants, as illustrated by our results from central Saskatchewan and by other works (e.g., Szepanski et al., 1999; Bocherens, 2000; Ben-David et al., 2001; Urton and Hobson, 2005). However, the $\delta^{13}C$ values of reindeer were significantly lower when they fed in a closed canopy environment. Therefore, the contrast between open and closed environment is clearly reflected in the $\delta^{13}C$ values of ruminants, independently of their forage preferences.

Our conclusions seem to contradict those presented by Stevens et al. (2006) based on the carbon isotopic study of five European populations of red deer. In their study, the results did not show any significant differences in $\delta^{13}C$ values although the studied populations lived under different environmental conditions. Moreover, the $\delta^{13}C$ values obtained for red deer populations living in open environments were claimed to be similar to those of the red deer from the closed forest of Bialowieza. However, several problems with the study of Stevens et al. (2006) make its conclusions problematic. First, the samples were collected between 1986 and 2002, but no correction for the shift in the $\delta^{13}C$ values of atmospheric CO_2 during this period was performed. As illustrated by Long et al. (2005), such corrections are

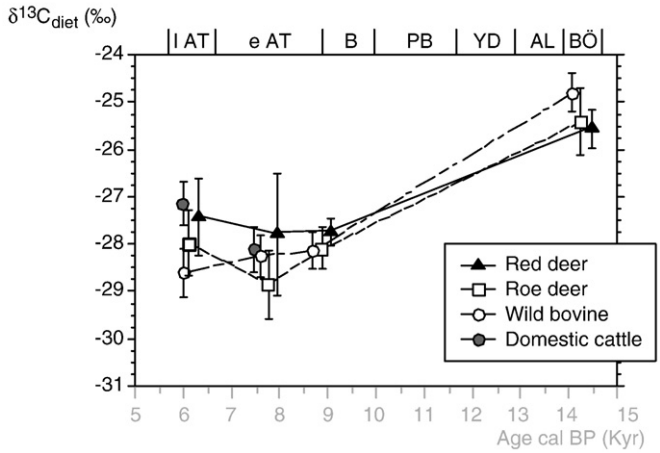

Fig. 4. Mean $\delta^{13}C_{diet}$ values of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild bovine (*Bos* or *Bison*) and domestic cattle (*Bos taurus*) from the Paris Basin during the Late-Glacial/Early Holocene transition. BÖ stands for Bölling, AL stands for Alleröd, YD stands for Younger Dryas, PB stands for Preboreal, B stands for Boreal, e AT stands for early Atlantic and l AT stands for late Atlantic.

necessary for reliable ecological studies based on carbon stable isotopes. Moreover, the obtained $\delta^{13}C$ values were confronted to the $\delta^{13}C$ values on red deer from Bialowieza Forest published by Bocherens and Drucker (2003), which were not directly comparable to modern data since they were set to Late Pleistocene $\delta^{13}C$ values of atmospheric CO_2. A second problem was the environment of the studied deer populations, for which the degree of closeness of the habitat is loosely described. Moreover, none of these sites correspond to a real dense forest, since the only site considered as "forest environment" was a conifer plantation. Unfortunately, in this type of plantation, ^{13}C depletion in understorey vegetation has been shown to be sometimes lacking due to well-ventilated conditions (e.g., France, 1996; Roche, 1999). One additional point is the fact that Stevens et al. (2006) does not discuss the possible impact of anthropogenic disturbance on red deer ecology in the considered environments. For instance, the deer population from Exmoor is known to cause heavy damage on cultivated crops (e.g. Langbein, 1997; Backshall, 2001; Langbein and Rutter, 2003). In such a context, individuals consuming more crop food than others would exhibit an increase in $\delta^{13}C$ values since the cultivated plant food growing in open environments present more positive $\delta^{13}C$ values than plants growing under a forest canopy, which could explain the large range of carbon isotopic values measured in this population.

We therefore still consider that the canopy effect has a significant impact on the $\delta^{13}C$ values of herbivores dwelling under closed forest conditions, in boreal and temperate contexts.

5.2. Late-Glacial–Early Holocene transition

The $\delta^{13}C_{diet}$ values of prehistoric large herbivores from Paris Basin, Jura and northern Alps exhibit a decrease of about 3‰ during the Late-Glacial/Early Holocene transition as previously described in several studies (Drucker et al., 2003; Richards and Hedges, 2003; Stevens and Hedges, 2004; Noe-Nygaard et al., 2005). All these studies agree that the decrease in $\delta^{13}C$ values of herbivores was clearly related to a decrease in $\delta^{13}C$ values in the consumed plants. It is therefore crucial to investigate the vegetational changes that occurred during this transition in the studied areas in connection to the observed patterns in herbivore $\delta^{13}C$ values.

Based on local palaeobotanical and geomorphological studies, the evolution of vegetation in the Paris Basin begins with an increase in arboreal species during the Bölling, but with still a relatively open plant cover and discontinuous woodland (Pastre et al., 2003). After the cold phase of Younger Dryas, the development of deciduous forests starts again during the Preboreal and becomes stable during the Boreal, around 9000 cal BP. These dense forests remain dominant during the early Atlantic and recent Atlantic, despite some local deforestation by Neolithic populations (Pastre et al., 2002). The general evolution of $\delta^{13}C$ values in Late-Glacial and early Holocene ungulates from the Paris Basin is in keeping with such an evolution of the vegetation cover documented by other approaches, and therefore seem to monitor the increase of the canopy effect during the forest development.

The evolution of vegetation during the Late-Glacial and early Holocene in Jura is documented with great detail, thanks to numerous lake sediment studies (e.g., Peyron et al., 2005; Magny et al., 2006). Shrub vegetation develops at the beginning of the Bölling, followed by the development of open pine–birch woodland. An expansion of open habitats occurs during the cold phase of the Younger Dryas, to the detriment of pine–birch woodland. This woodland environment develops again at the Younger Dryas–Preboreal transition, and meso–thermophilous species, such as hazel, oak and elm, increase in abundance during the Boreal period, when forests of temperate type start to stabilize. Red deer clearly exhibit more positive $\delta^{13}C$ values during the Late-Glacial periods, when plant cover was shrub

Table 6
Isotopic results for ancient red deer from the Jura

Lab n°	Site	Altitude (m asl)	Sample	Excavation n°	Level	C_{coll} (%)	N_{coll} (%)	C/N_{coll}	$\delta^{13}C_{coll}$ (‰)	$\delta^{13}C_{diet}$ (‰)	Age conv. BP (lab ref)	Age cal BP
RCD500	Rochedane	355	Left radius	D6 Roch70 n°19	D1	42.3	15.5	3.2	−19.9	−25.0	12250±70 (GrA21512)	13,902–14,510
RCD1000	Rochedane	355	Left metatarsal	H9–G9	C'1	42.5	15.4	3.2	−20.7	−25.8	11,570±70 (GrA21514)	13,270–13,605
RCD2600	Rochedane	355	Left metatarsal		B	38.8	14.0	3.2	−20.0	−25.1	11,600±80 (GrA21516)	13,282–13,650
RCD4700	Rochedane	355	Left metatarsal	F9-186	A4	39.7	14.8	3.1	−19.5	−24.6	10,880±50 (GrA23147)	12,815–12,917
RCD4800	Rochedane	355	Left metatarsal	H9-190-195	A4	40.7	14.7	3.2	−20.6	−25.7	10,830±70 (GrA21518)	12,747–12,923
RCD6300	Rochedane	355	Left metatarsal	H8	A3	39.1	14.3	3.2	−23.4	−28.5	8640±60 (GrA21519)	9500–9772
RCD6400	Rochedane	355	Left metatarsal		A3	36.8	13.4	3.2	−21.5	−26.6	10,880±50 (GrA23150)	12,815–12,917
RCD10100	Rochedane	355	Left metatarsal	F11-12-135-140	A2	37.4	13.5	3.2	−22.8	−27.9	6730±60 (GrA21520)	7490–7679
RCD10500	Rochedane	355	Right metacarpal	Ro72 F10-11 121	A1	42.2	16.5	3.0	−23.6	−28.7	6230±60 (GrA21522)	6976–7269
BVN-2	Bavans	275	Right talus	86 π2 déc12 n°13	5	37.9	13.3	3.3	−23.0	−28.1	6000±60 (GrA22131)	6677–6987
BVN-7	Bavans	275	Metatarsal	O4 déc20	7	26.1	9.8	3.1	−23.4	−28.5	6935±40 (GrA23127)	7677–7913
BVN-9	Bavans	275	Jawbone	γ8-156-160 no. 5	terre jaune	25.9	9.6	3.2	−20.8	−25.9	12,170±60 (GrA23129)	13,857–14,171
RAN-2	Ranchot	216	Left radius	RAN 89 Zg 258	AOC	44.7	15.8	3.3	−23.6	−28.7	8570±60 (GrA21524)	9470–9674
RAN-5	Ranchot	216	Left radius	RAN 89 A11 402	AOC	42.7	15.2	3.3	−24.0	−29.1	8840±60 (GrA21529)	9771–9948
RAN-8(2)	Ranchot	216	Left scapula	RAN 83 I11 125<z<132	AC	37.3	13.9	3.1	−21.9	−27.0	8380±45 (GrA23149)	9289–9491
RAN-9(2)	Ranchot	216	Left scapula	RAN 85 G10 112	AC	36.8	13.6	3.1	−22.9	−28.0	8300±45 (GrA25193)	9136–9435

Tissue $\delta^{13}C_{coll}$ values correspond to $\delta^{13}C$ values measured on collagen; $\delta^{13}C_{diet}$ values correspond to the $\delta^{13}C_{coll}$ values −5.1‰. The radiocarbon dates (Age conv. BP) were calibrated to cal years BP using the IntCal04 calibration dataset (Reimer et al., 2004).

Table 7
Isotopic results for ancient red deer from the Northern Alps`

Lab n°	Site	Altitude (m asl)	Sample	Excavation n°	Level	C_{coll} (%)	N_{coll} (%)	C/N_{coll}	$\delta^{13}C_{coll}$ (‰)	$\delta^{13}C_{diet}$ (‰)	Age conv. BP	Age cal BP
FRU-1	La Fru	570	Metatarsal	Fru III M71 68	III-2	38.1	13.7	3.2	−20.1	−25.2	9940±50 (GrA23130)	11,238–11,607
FRU-2	La Fru	570	Right metacarpal	Fru III K70 14	III-3	35.2	13.7	3.0	−22.4	−27.5	8630±70 (GrA22134)	9485–9885
FRU-3	La Fru	570	Right metacarpal	Fru III K70 63I	III-4a	32.7	12.4	3.1	−21.1	−26.2	9490±70 (GrA22116)	10,574–11,089
FRU-9	La Fru	570	Right metacarpal	Fru III L70 354	III-4a	39.4	14.8	3.1	−20.2	−25.3	8630±70 (GrA25061)	9485–9885
FRU-4	La Fru	570	Phalanx I	Fru III L72 591	III-4c	29.5	11.6	3.0	−20.8	−25.9	11420±60 (GrA25062)	13,173–13,401
FRU-5	La Fru	570	Left talus	Fru III K70 1336	III-7	36.3	14.1	3.0	−20.3	−25.4	12260±90 (GrA22098)	13,883–14,648
FRU-10	La Fru	570	Left metacarpal	Fru I F24 129 c1c	I-1c	43.7	16.0	3.2	−19.9	−25.0	11950±60 (GrA25052)	13,692–13,964
FRU-13	La Fru	570	Left metacarpal	Fru I F25 386 c1c	I-1c	43.3	16.0	3.2	−20.2	−25.3	11790±60 (GrA25054)	13,465–13,780
FRU-15	La Fru	570	Left metacarpal	Fru I A9 QAOB FC 7	I-3?	42.7	15.9	3.1	−21.1	−26.2	11840±60 (GrA25060)	13,536–13,835
LDT200	Les Douattes	370	Inf P4	F5-73		41.7	15.3	3.2	−20.7	−25.8	12100±60 (Ly14530OxA)	13,806–14,095
LDT600	Les Douattes	370	Metatarsal	D99 F554		41.8	15.4	3.2	−19.8	−24.9	12570±80 (GrA22132)	14,272–15,085
APS-2	Aulp-du-Seuil	1700	Right tibia	ALP1 F6 300	C2 sup	42.9	15.9	3.2	−21.7	−26.8	7110±50 (GrA24775)	7841–8015
GRV-1	La Grande Rivoire	580	Tibia	178	D	42.1	15.3	3.2	−20.4	−25.5	9160±50 (GrA25064)	10,230–10,487
GRV-5	La Grande Rivoire	580	Phalanx	2C	C	41.4	15.1	3.2	−21.1	−26.2	8640±50 (GrA25065)	9528–9731
GRV-9	La Grande Rivoire	580	Tibia	GRiv-6 55 B3	B3	41.8	15.6	3.1	−21.1	−26.2	7435±45 (GrA25066)	8178–8357

Tissue $\delta^{13}C_{coll}$ values correspond to $\delta^{13}C$ values measured on collagen; $\delta^{13}C_{diet}$ values correspond to the $\delta^{13}C_{coll}$ values +5.1‰. The radiocarbon dates (Age conv. BP) were calibrated to cal years BP using the IntCal04 calibration dataset (Reimer et al., 2004).

vegetation and open woodland, than during the Early Holocene, when vegetation corresponds to dense temperate forest.

Less data are available for the French northern Alps than for Jura, but the evolution of vegetation in the Alps looks broadly similar to that of Jura. The development of forest starts during the Preboreal, with an upper tree limit higher than 2100 m during the Holocene (Tessier et al., 1993). In contrast to the Jura red deer, those from the French Northern Alps did not exhibit a significant decrease of their $\delta^{13}C$ values, despite the change of vegetation that occurred below 2000 m. This situation exemplifies the possible role of local parameters, in such case the range of altitudes around the sites corresponding to a range of vegetation type, from dense forests at lower altitudes and more open plant formations at higher altitudes, that can significantly impact the $\delta^{13}C$ values of large herbivores.

We consider that the canopy effect linked to the increasing forest cover in western Europe is a convincing driving parameter for the observed decline in $\delta^{13}C$ value of herbivores at the transition between Late-Glacial and Early Holocene. However, besides the canopy effect, more global factors such as the increase in atmospheric CO_2 concentration has been suggested as the main cause for the decline in $\delta^{13}C$ values (Richards and Hedges, 2003; Hedges et al., 2004; Stevens and Hedges, 2004). Their conclusions were inspired by the work of Leavitt and Danzer (1992) who considered increasing atmospheric CO_2 concentration during the Late-Glacial (Neftel et al., 1988; Smith et al., 1997) as responsible for observed decreasing plant $\delta^{13}C$ values by 1 to 4‰ (Krishnamurthy and Epstein, 1990; Leavitt and Danzer, 1991; van de Water et al., 1994). This hypothesis was supported by experimental results of Poley et al. (1993) who observed such a shift in plants facing an increase in atmospheric CO_2 concentration. However, contrary to Poley et al. (1993), experimental work of Arens et al. (2000) concluded that $\delta^{13}C$ values of plants depended mainly on $\delta^{13}C$ values of atmospheric CO_2. Indeed, plants seem able to adapt their stomatal conductance to variation in atmospheric CO_2 concentration and so maintain the same isotopic discrimination against ^{13}C (see Ehleringer and Cerling, 1995). In a context of a constant $\delta^{13}C$ value of atmospheric CO_2, environmental conditions would be primarily influenced by environmental and plant growth-form parameters (Arens et al., 2000). Therefore, increase in atmospheric CO_2 is unlikely to be responsible for the observed trend in herbivore $\delta^{13}C$ values at the Late-Glacial to Early Holocene transition.

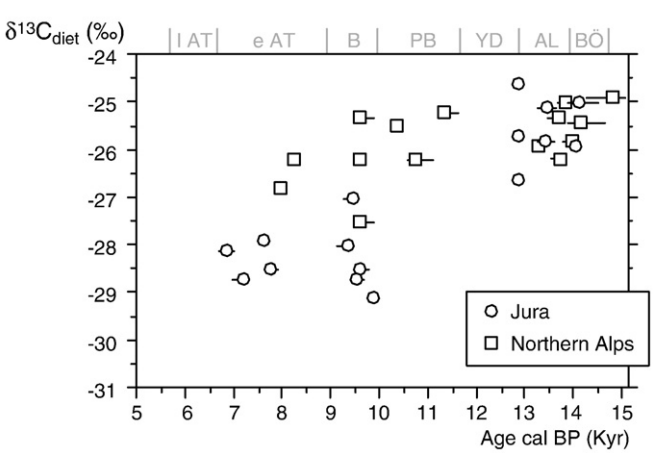

Fig. 5. $\delta^{13}C_{diet}$ values of red deer (*Cervus elaphus*) from the Jura and the northern Alps during the Late-Glacial/Early Holocene transition. BÖ stands for Bölling, AL for Alleröd, YD for Younger Dryas, PB for Preboreal, B for Boreal, e AT for early Atlantic and l AT for late Atlantic. The horizontal bars correspond to the range of 2 standard-deviations for the calibrated radiocarbon dates if they exceed the size of the circle or square.

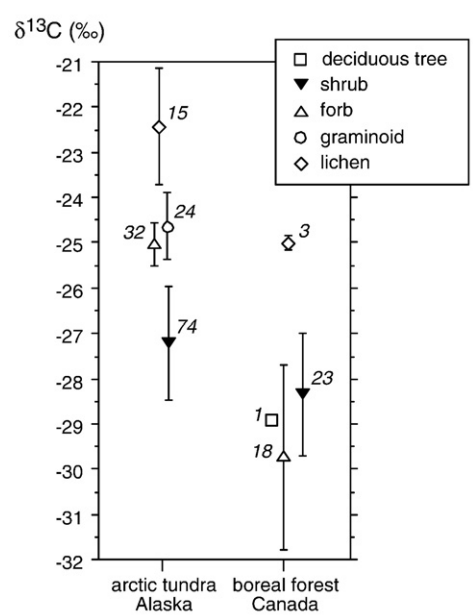

Fig. 6. Comparison of $\delta^{13}C$ values of plant types in open (tundra: Barnett, 1994) and closed canopy (boreal forest: Brooks et al., 1997) environments. For the boreal forest, only plants growing under 3 meters from the soil are considered since they are the ones reachable to the studied herbivore species. Number of specimens (n) are given. Data for lichen from boreal lichen are unpublished.

Moreover, there is a chronological discrepancy between the most important increase in atmospheric CO_2, that occurs at the end of the Pleistocene and well before the beginning of the Holocene (Smith et al., 1999), and the observed decrease in herbivore $\delta^{13}C$ values that occur at the beginning of the Holocene.

Also based on a critical reappraisal of the possible impact of atmospheric CO_2 on plant $\delta^{13}C$ values, Hedges et al. (2006) finally consider the drop in $\delta^{13}C$ values of large mammals at the Late-Glacial to Early Holocene transition as the result of the combination of different environmental and climatic parameters. Among these parameters, forest development was mentioned as a minor component, principally because changes in faunal collagen $\delta^{13}C$ values were considered to be similar among species and between geographical regions. However, the isotopic data that we present in this paper contradict this pattern.

Indeed, the depletion in $\delta^{13}C_{diet}$ values we observed in Paris Basin during the Late-Glacial/Early Holocene transition (ca. 15,000–6000 yr cal BP) differed among species. Differences in $\delta^{13}C_{diet}$ values decline pattern among wild bovine, red and roe deer was probably due to species-related change in diet and adaptation to a changing environment. Domestic cattle and wild bovine have the same digestive physiology and, indeed, exhibited comparable $\delta^{13}C_{diet}$ values during the early Atlantic. In the late Atlantic, however, cattle $\delta^{13}C_{diet}$ values increased toward higher values than those of wild bovine. If we consider the depleted $\delta^{13}C_{diet}$ values of wild bovine as the result of under canopy feeding, this could indicate an access to open areas for cattle bred by Middle Neolithic humans. The same pattern of $\delta^{13}C$ values being less depleted in late Atlantic domestic cattle than in contemporaneous aurochs was observed in Denmark by Noe-Nygaard et al. (2005) and in the French Jura by Bocherens et al. (in press). This pattern in decline of $\delta^{13}C$ values depending on the considered species suggests that it is due not only to dietary preferences, but also to niche partitioning involving differences in habitat (Stewart et al., 2003).

Finally, red deer from Jura and northern Alps confirm that local differences in patterns of change in $\delta^{13}C_{diet}$ values of a single species occurred during the Late-Glacial/Early Holocene transition. We interpret this isotopic difference as the result of differences in the extent of forest canopy development in the red deer habitat over time and space. In Jura, red deer $\delta^{13}C_{diet}$ values, were more depleted after the Younger Dryas than before. This decrease in red deer $\delta^{13}C_{diet}$ values over time was consistent with the development of dense deciduous forests composed of hazelnut (*Corylus*), oak (*Quercus*) and elm (*Ulmus*) at the end of the Preboreal as shown by pollen analysis (Richard et al., 2000). The northern Alps area yielded higher $\delta^{13}C_{diet}$ values through the Late-Glacial/Early Holocene transition. This can be explained by the presence of habitat more exposed in this region than in Jura, probably linked to the high altitude of the sites (from 370 to 1700 m) and their surroundings. Although $\delta^{13}C$ values of plants have been shown to increase with altitude at a rate of 0.7‰ / 1000 m (Körner et al., 1988). Thus, a difference in altitude of more than 3000 meters would be required to account for the observed difference in red deer $\delta^{13}C$ values between Jura and northern Alps, all other parameters being equal. The mere altitude difference is therefore not sufficient to explain the observed trend. A much more likely explanation is the environmental contrast between the studied sites of Jura and those from the Alps. Indeed, the sites of Jura are located in the Doubs valley less than 360 m asl and are connected largely with adjacent plains where the dense canopy forest could have spread more rapidly than in the Northern Alps sites where red deer were hunted.

6. Conclusion

The study of well-monitored free-ranging populations of cervids and bovines confirms that the carbon isotope signatures of ruminants can reflect the canopy effect. This allows, in pure C_3 environments, to distinguish herbivore populations feeding under closed canopy forests from populations feeding in more open environments. It is important to bear in mind that the so called "canopy effect" results from the convergent effects of particular conditions, involving abiotic factors, such as temperature, humidity, and air circulation, as well as biotic factors, such as the floristic composition, growth stage and canopy complexity. Not all woodland types will generate a canopy effect. However, when a canopy effect is observed, it implies the occurrence of mature, dense and complex forest stands. Having a natural tracker of the development of such environments, the carbon isotope composition of large herbivore tissues, allows to complement the other palaeoenvironmental tracers, especially palaeobotanical ones. In ancient contexts of forest expansion, such as the Late-Glacial to Early Holocene transition, it offers a means to document the habitat shift of herbivores hunted by prehistoric populations, and to compare patterns of environmental change during this period of global warming.

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