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Soil and vegetation nutrient response to bison carcasses in Białowieża Primeval Forest, Poland

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Abstract Ungulate carcasses can have important effects on the surrounding soil and vegetation. The impact of six carcasses of European bison (*Bison bonasus*) was investigated for the first time in a natural temperate forest (Białowieża, Poland) by measuring soil and plant nutrient concentrations along a gradient extending from the centre of each carcass. Calcium concentration and pH were found to be higher at the centre of the carcass, decreasing towards the periphery. This effect lasted up to 7 years after the death of the animal. The concentration of most nutrients in the soil and plants varied irregularly, suggesting an effect of the carcass at its centre but the absence of a clear pattern of variation along the gradient. Concentrations of NO_3^- in the soil differed only at the 1-year old carcass, suggesting a fast turnover of nitrate in temperate forests. Our results show that the effects of large herbivore carcasses on soil and plant nutrient concentrations are not easily detectable in a temperate forest as in more homogeneous habitats, such as tundra and prairie. This may be due to the high activity of scavengers and nutrient recycling in the study area, but it may also be a consequence of a more com-

plex and patchy interaction between nutrient availability and other limiting factors in temperate forests.

Keywords *Bison bonasus* · Carrion · Decomposition · Disturbance · Nitrogen · Nutrient recycling · Scavengers

Introduction

Large herbivores are widely recognised to strongly influence soil processes and the structure and diversity of plant communities (Hobbs 1996; Augustine and McNaughton 1998; van der Wal et al. 2004). They can affect vegetation directly by grazing or indirectly by changing the turnover rates of nutrients. Herbivores play a keystone role in nitrogen (N) turnover; they recycle N by eating plants and redistributing it through faeces and urine (Hobbs 1996), causing an increase or a decrease in plant available N. Thus, they can increase the patchiness of N availability, and their impact on plant distribution and growth can be measured (McKendrick et al. 1980). However, the most striking impact of herbivores on the ecosystem occurs after death, when their carcasses not only subsidise the food supply of many vertebrate scavengers (Selva et al. 2003, 2005) but also release a local and highly concentrated pulse of nutrients into the soil (Danell et al. 2002). Thus, an ungulate carcass represents a natural disturbance and a potentially significant source of nutrient enrichment, which can have important effects on the heterogeneity and diversity of plant communities (Towne 2000; Danell et al. 2002).

Whereas much literature has dealt with the nutrient contribution of carcasses of migratory fish in ecosystems (e.g. Cederholm et al. 1999), the effect of terrestrial vertebrate carcasses on nutrient pools and fluxes remains relatively unexplored. The impact of large herbivore carcasses on soil and plant nutrient concentration has been measured in the North American prairie for American bison (*Bison bison*), cattle (*Bos taurus*) and

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deer (*Odocoileus virginianus*) (Towne 2000) and in the Canadian arctic tundra for muskox (*Ovibos moschatus*) (Danell et al. 2002), but no quantitative data exist for temperate forest. In both prairie and tundra the effect of large herbivore carcasses on the surrounding vegetation was found to be dramatic, lasting for several years. Inorganic N concentrations were significantly higher both in the soil (Towne 2000) and vegetation (Danell et al. 2002) around the carcass sites, declining along a gradient the further from the carcass. Even in relatively homogeneous environments, such as the prairie and tundra, ungulate carcass sites remained disturbed patches for several years, supporting different vegetation than the surroundings. In grassland ecosystems N availability frequently limits plant productivity (Towne 2000), whereas in the arctic nutrient cycling is severely slowed by low temperatures, short summers and low water availability (Danell et al. 2002).

Carrion recycling by decomposers and vertebrate scavengers causes nutrient input in the soil at the carcass site but also transfers nutrients to other areas. In temperate ecosystems, air temperature is the main factor mediating carcass acquisition by scavengers or decomposers. In fact, it determines whether most of the carrion is subjected to microbial and invertebrate decomposition, thus infusing the soil under the carcass with nutrients, or whether it is mainly consumed by scavengers, thereby spreading the carcass nutrients over wider areas (DeVault et al. 2004; Selva et al. 2005). However, several studies have demonstrated that, across all climatic zones, vertebrates are responsible for the bulk of the consumption of available carcasses in terrestrial habitats (see DeVault et al. 2003 for a review). Thus, most of the nutrients are scattered, and the effect of decomposition at the carcass site itself may be rather limited.

In a natural temperate forest like Białowieża Primeval Forest, eastern Poland, the supply of ungulate carcasses is especially abundant during the winter, and many species of birds and mammals rely on carrion resources (Selva 2004). However, winter carcasses of large ungulates can persist for several months, attracting large numbers of scavengers whose faeces and urine may add to the further build-up of nutrients. These carcasses usually last until spring, when decomposers finally clean up the last remains (Selva et al. 2003), although decomposition can also take place in winter, depending on temperature (Nabagło 1973). The aim of the present study was to determine whether carcasses of large ungulates have any effect on the concentration of soil and vegetation nutrients in a natural temperate forest that is rich in nutrients and supports a diverse community of scavengers and decomposers and, if so, determine how long these effects last. We therefore investigated the impact of carcasses of the largest herbivore found in European temperate forest, the European bison (*Bison bonasus*), by measuring the concentration of soil and vegetation nutrients along a gradient extending from the centre of the carcass.

Methods

Study area

The study was conducted in the Polish part of the Białowieża Primeval Forest (BPF; 595 km², 52°45'N, 24°E). BPF covers a total of 1450 km² and is located on the Poland-Belarus border. It is one of the best preserved lowland forests of its size in temperate Europe. The main tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus silvestris*), oak (*Quercus robur*), hornbeam (*Carpinus betulus*), black alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) and birches (*Betula verrucosa* and *B. pubescens*). The terrain is flat and the elevation varies between 134 and 186 m a.s.l. The only open areas within the woodland are marshes of sedge (*Carex* spp.) and reed (*Phragmites australis*). Five species of ungulates live in the BPF. The most numerous are red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*); less common are roe deer (*Capreolus capreolus*), European bison and moose (*Alces alces*). Large predators include the lynx (*Lynx lynx*) and the wolf (*Canis lupus*). Important scavengers are the wolf, red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), raven (*Corvus corax*) and common buzzard (*Buteo buteo*). More information on BPF and the vertebrate community is provided by Jędrzejewska and Jędrzejewski (1998).

During the study period, 250–310 bison lived in the Polish part of the BPF (density: 0.4–0.5 individuals/km²). To keep the population within the carrying capacity of the forest, bison are regularly culled, and operation which takes place during the winter (about 10% of the population). Each year a few of the culled bison are removed from the forest and deposited in some open areas traditionally used as dumps for dead animals for hunting purposes. The natural mortality of free-living bison is quite low, 3% on average (Kraśniński et al. 1994), and they are occasionally preyed upon by wolves (Jędrzejewski et al. 2002). Thus, natural bison carcasses are rare and not easy to find in the forest. In one of the few reported studies on bison carcasses, Selva et al. (2003) monitored the utilisation by scavengers of the carcasses of five adult bison that died naturally during a 7-year period from the winter of 1997–1998 to the spring of 2001. They found a sixth carcass in the BPF during sampling and that was aged 1 year, but its utilisation by scavengers was not known in detail. Selva et al. (2003) estimated that the average body mass of a bison carcass was 419 ± 119 kg, of which about 87% was removed, mainly by scavengers. On average, the complete depletion of a bison carcass took about 4 months. These researchers recorded a total of 13 birds and mammals species feeding on bison carcasses in the BPF, among which the main scavengers in forest habitats were raven, red fox, wolf, common buzzard and raccoon dog. Only wolves could open intact bison carcasses, thus facilitating scavenging by other species. Wolves repeatedly

visited bison carcasses and often dragged them once the bulk of the mass was removed.

Sampling at carcass sites

All six carcasses were located in the forest (Table 1). We did not sample the carcasses exposed by hunters in the open areas because these areas were used as artificial feeding sites for bison and other ungulates, which infused the soil with nutrients through faeces and urines. Moreover, the exact position and time of influence of each of these carcasses were difficult to identify, since several carcasses had been exposed close to each other over many years. After scavengers had removed most of the meat from the studied carcasses, the approximate centre of the carcass site was marked permanently with a banner.

Soil and vegetation samples were collected during the late summer of 2004. Soil nutrient levels surrounding the carcasses were determined by collecting two core samples at a depth of 10 cm in opposite directions at 0, 1, 2, 4, and 20 m from the centre. The sample that was taken at 20 m from the carcass was considered to be unaffected by the carcass and used as a control. As a bison carcass is approximately 2 m in diameter, we can therefore consider the area from 0 to 1 m around the centre of the carcass to be under its direct influence. However, this could also depend on the activities of the scavengers (e.g. dragging by wolves). We collected green fresh leaves (approx. 30 for each sample) from the most common ground-layer species at each carcass site, normally *Hepatica triloba* and *Oxalis acetosella*. At one carcass site we collected *Vaccinium myrtillus*, since it was the only species present at every sampling distance (Table 1).

A total of 52 soil and 52 vegetation samples were analysed by the Wageningen University Testing Laboratory of the Resource Ecology Group. In plant leaves the total N, total phosphorous (P), sodium (Na), potassium (K), calcium (Ca) and magnesium (Mg) were determined by digestion with H₂SO₄-Se-salicylicid-H₂O₂. In soil total N, total P and Ca were determined by digestion with H₂SO₄-Se-salicylicid-H₂O₂. Inorganic nitrogen (NO₃⁻, NH₄⁺), PO₄⁻, Na, Mg and K in soil were

determined by extraction with CaCl₂. The pH of the soil was also measured during the extraction (before filtration). The C/N ratio in the soil and vegetation was determined on a CN analyser (CHN-0; Fisons, Woodstock, Ill.). The total N, total P, inorganic nitrogen (NO₃⁻, NH₄⁺) and inorganic phosphorous (PO₄⁻) in soil and vegetation were measured with an autoanalyser (Skalar San Plus, colorimetric system), while K, Ca, Mg and Na were measured with an Atomic Absorption Spectrometer (SpectrAA-600; Palo Alto, Calif.).

Data analysis

Percentages of C and N were square-root-arcsine-transformed. Other response variables were log- or square root-transformed to reduce skewness and improve normality. All response variables were checked for normality following the removal of outliers (D'Agostino normality test, $P > 0.05$; D'Agostino and Stephens 1986). For both soil and plant samples, we used multiple linear regression to analyse the relationship between the concentration of a particular nutrient, carcass age (as numbers of years elapsed since bison death) and distance from the centre of the carcass. The variable 'site' was always set as a covariate to account for unexplained variation in the nutrient concentration associated with a given site. We used the Akaike Information Criterion (AIC) corrected for small samples (AIC_c; Burnham and Anderson 2002) to select the most parsimonious model. Only those estimates of the models with a ΔAIC_c (i.e. difference in Akaike values between the first and the actual model) lower than 2 that included the variable 'distance' are shown (Burnham and Anderson 2002). Statistical significance for all tests was accepted at $P < 0.05$. Data were analyzed using R 2.0.2 Software® (Development Core Team 2004).

Results

Soil nutrient concentration

Site and distance from the centre of the carcass were the most important variables explaining the variation in pH

Table 1 Bison carcasses sampled in the Białowieża Primeval Forest (BPF) in 2004

Site ^a	Year of death	Age ^b	Season	Forest type	Vegetation sampled	Dominating tree layer	Dominating ground layer
103C	1997	7	Cold	Mixed coniferous	<i>Oxalis acetosella</i> , <i>Hepatica triloba</i>	<i>Picea abies</i>	<i>Oxalis acetosella</i> , <i>Hepatica triloba</i>
40A	1998	6	Warm	Deciduous	<i>Oxalis acetosella</i>	<i>Carpinus betulus</i>	<i>Oxalis acetosella</i>
187C	1999	5	Cold	Mixed coniferous	<i>Vaccinium myrtillus</i>	<i>Picea abies</i>	<i>Vaccinium myrtillus</i>
389A	2000	4	Cold	Mixed coniferous	<i>Hepatica triloba</i> , <i>Oxalis acetosella</i>	<i>Picea abies</i>	<i>Hepatica triloba</i>
394C	2001	3	Cold	Mixed coniferous	<i>Oxalis acetosella</i>	<i>Picea abies</i>	<i>Oxalis acetosella</i>
394C	2003	1	Cold	Mixed coniferous	<i>Oxalis acetosella</i>	<i>Picea abies</i>	<i>Oxalis acetosella</i>

^a Site refers to the local cartographic system

^b Age refers to the number of years from the death of the animal

Table 2 Set of linear regression models of pH (log-transformed) of soil, Ca concentration (log-transformed) in soil, NO₃⁻ concentration (square root-transformed) in soil and Na concentration (square root-transformed) in *Oxalis acetosella*

Model ^a	K ^b	R ²	AIC _c	ΔAIC _c	ω _i ^d
pH					
Site + distance	7	0.75	-97.37	0.00	0.76
Age + site + distance	8	0.75	-94.67	2.70	0.20
Site	6	0.72	-90.97	6.39	0.03
Age + site	7	0.71	-88.38	9.99	0.01
[Ca] (mg/kg)					
Site + distance	7	0.27	107.40	0.00	0.59
Age + site + distance	8	0.27	108.60	1.25	0.31
Distance	3	0.12	112.30	4.95	0.05
Age + distance	4	0.14	112.50	5.07	0.05
[NO₃⁻] (mg/kg)					
Age	3	0.46	138.38	0.00	0.58
Age + distance	4	0.46	139.35	0.97	0.36
Age + site	7	0.46	143.70	5.29	0.04
Age + site + distance	8	0.46	144.91	6.53	0.02
[Na] (mmol/kg)					
Age	3	0.30	146.20	0.00	0.74
Age + distance	4	0.28	148.50	2.30	0.23
Site	5	0.18	154.90	8.70	0.02
Site + distance	6	0.16	157.60	11.40	0.01

^a The explanatory variable 'distance' was square root-transformed. The models were ranked by the AIC_c corrected Akaike Information Criterion (AIC). The most parsimonious models are on the top of each list

^b K, Number of parameters

^c ΔAIC_c, Difference in Akaike values between the first and the actual model

^d ω_i, Akaike's weights, i.e. normalized likelihoods of the models

(Tables 2, 3; Adjusted R² = 0.74, df = 52, P < 0.0001), which was higher in the centre of the carcass at almost all carcass sites, decreasing along the gradient. This pattern was evident from 1 up to 6 years after death (mean ± SD at 0 m = 4.09 ± 1.15; at 1 m = 3.59 ± 0.59; at 2 m = 3.50 ± 0.83; at 4 m = 3.52 ± 0.77; at 20 m = 3.30 ± 0.52).

Carcass presence affected the concentration of Ca and NO₃⁻ in the soil. Levels of Ca were also influenced by site and distance from the centre of the carcass (Tables 2b, 3b; Adjusted-R² = 0.25, df = 52, P < 0.001), but during the first year after death no differences in Ca concentration were detected across distances (Fig. 1a). Data were not available on 2-year-old carcasses, but 3 years after death there was a higher concentration of Ca at the carcass centre, decreasing towards the periphery. This gradient was still present after 6 years, but disappeared after 7 years, when no differences in Ca concentration were detected across distances (Fig. 1a).

For NO₃⁻ concentration, the variable 'distance' was not included in the most parsimonious model; however, the ΔAIC_c and the evidence ratio between the first and the second best model (including 'distance') were not so high as to clearly support the first model (Burnham and Anderson 2002). Therefore, we reported the estimates

Table 3 Estimates of the most parsimonious model, including distance of pH (log-transformed) of soil, Ca concentration (log-transformed) in soil, NO₃⁻ concentration (square root-transformed) in soil

Model terms	Estimate	Standard error	t-value	P
pH				
Intercept	1.42	0.03	41.69	***
Site 187C	-0.26	0.04	-5.83	***
Site 389A	-0.04	0.04	0.86	NS
Site 394C	-0.26	0.04	-6.89	***
Site 40A	0.14	0.04	3.33	**
Distance	-0.02	0.01	-2.95	**
[Ca] (mg/kg)				
Intercept	7.87	0.20	39.63	***
Site 187C	-0.48	0.26	-1.87	NS
Site 389A	-0.05	0.26	-0.19	NS
Site 394C	0.36	0.22	1.65	NS
Site 40A	0.19	0.25	0.76	NS
Distance	-0.16	0.05	-3.11	**
[NO₃⁻] (mg/kg)				
Intercept	2.73	0.27	10.19	***
Age	-0.34	0.05	-6.81	***
Distance	-0.14	0.07	-2.14	*

*P < 0.05, **P < 0.01, ***P < 0.001, NS > 0.05

for the model including both distance and age of the carcass (Tables 2, 3; Adjusted-R² = 0.46, df = 55, P < 0.001). NO₃⁻ concentration was higher at the centre of the carcass 1 year after the death of the animal, but in older carcasses we did not detect any difference across distances (Fig. 1b).

For the percentages of C, N, the C/N ratio and concentrations of K, P, Na, NH₄⁺ and PO₄⁻, distance was not included in the most parsimonious model when all of the samples were considered together. However, for some carcasses, K (Fig. 1c) and PO₄⁻ (Fig. 1d) concentrations were higher at the carcass centre than at other distances.

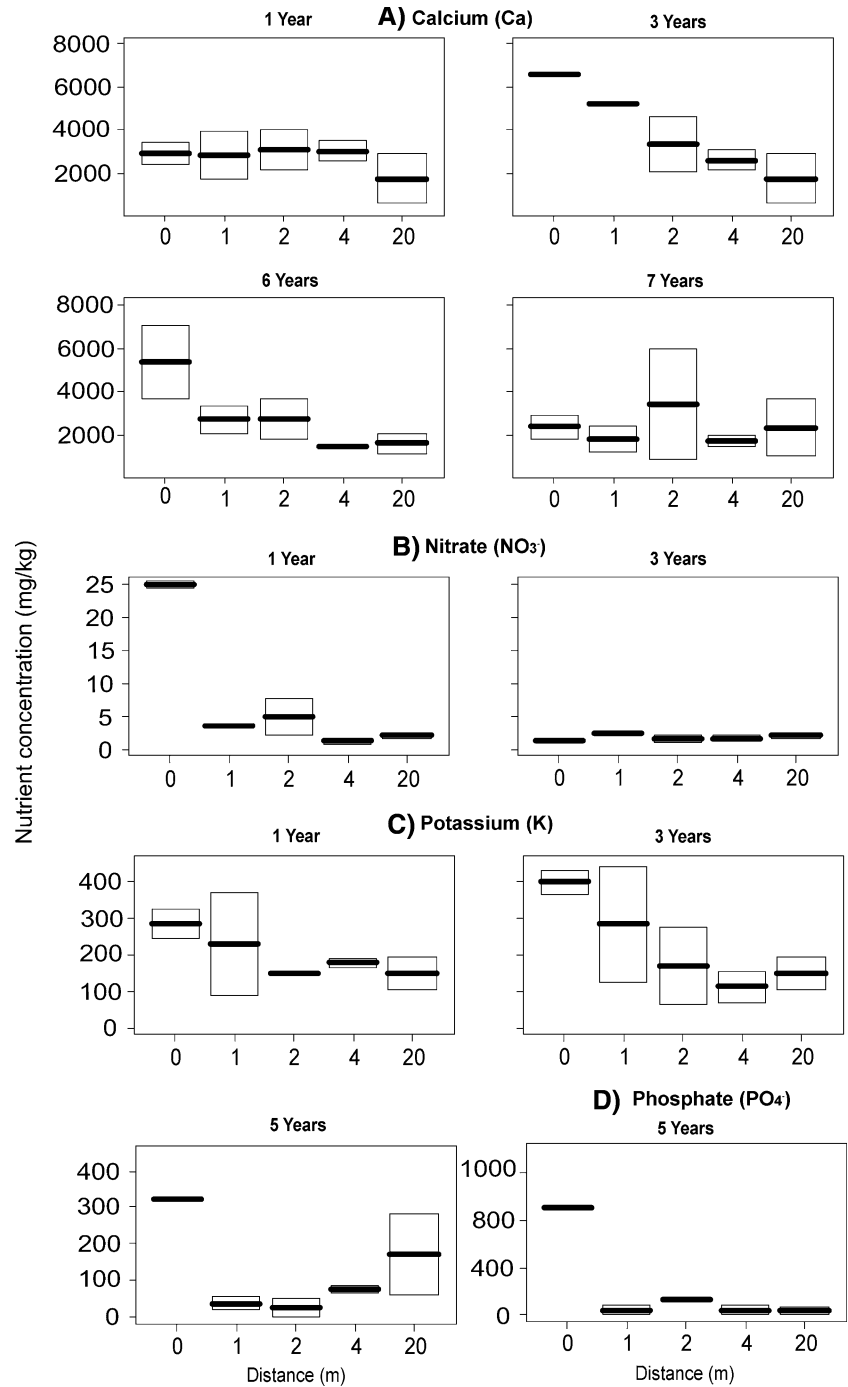
Vegetation nutrients concentration and species cover

Since there was a statistical effect of the specific plant species on the concentration of some nutrients, we decided to evaluate the factors affecting nutrient concentration separately for each species.

Oxalis acetosella was collected at five carcass sites (Table 1). For Na content, the variable 'distance' was not included in the most parsimonious model, but it was included in the second best (Table 2; Adjusted R² = 0.28, df = 34, P < 0.001), however, its contribution to the model was minimal, and both the delta Akaike and the Akaike's weight gave little support to this model. The plant concentrations of other nutrients were not affected by the variables distance and year, but there was always an effect of site.

Hepatica triloba was collected at two carcasses only and, therefore, statistical analyses were not possible.

Fig. 1 Box plots of the values of Ca (a), NO_3^- (b), K (c) and PO_4^- (d) concentrations measured in soil at progressive distances from the centre of bison carcasses of different ages in the Białowieża Primeval Forest (BPF). Twenty metres is the control value



Nevertheless, a threefold higher concentration of Na was detected at the centre of the 4-year-old carcass (Fig. 2). The concentrations of all of the other nutrients were constant over time and space.

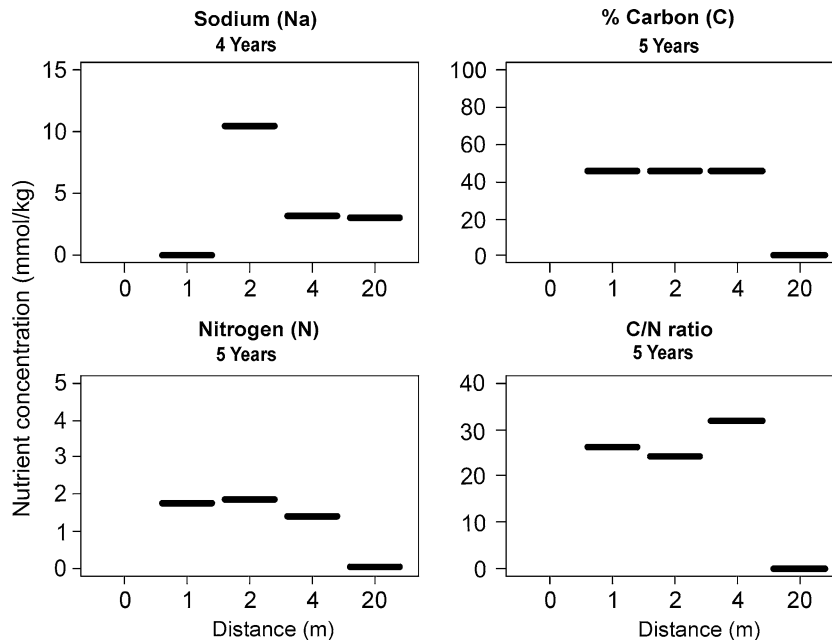
Vaccinium myrtillus was collected only at the 5-year-old carcass. The percentage of C, N and the C/N ratio were higher around the carcass than at 20 m distance (Fig. 2). None of the concentrations of other nutrients were explained by the variable 'distance'.

No difference in plant community composition or in plant height, abundance or diversity between carcass and the surrounding forest could be detected.

Discussion

The response of soil nutrients to bison carcasses was heterogeneous. At some carcasses the concentration of the nutrients varied along the gradient. However, the concentration of most nutrients varied irregularly, suggesting an effect of the carcass at its centre but not a clear pattern of variation along its gradient. An asymmetric response of soil nutrient concentration to carcasses was also found by Towne (2000) in prairie. One of the most evident effects of bison carcasses was on the

Fig. 2 Box plots of the values of Na (mmol/kg) measured in green leaves of *Hepatica triloba* collected at progressive distances from the centre of a 4-year-old bison carcass and the percentages of C and N and the C/N ratio measured in green leaves of *Vaccinium myrtillus* collected at progressive distances from the centre of a 5-year-old bison carcass in the BPF. Twenty metres is the control value



soil content of Ca, which was higher at carcass sites than in the surroundings from 3 to 6 years following the death of the animal; however, no difference in Ca concentration was detected 7 years after the death of the animal. The effect of the carcass on Ca levels in the soil may also depend on how many bones were scattered by scavengers and moved around throughout the years. Since we did not have replicates for each carcass of a specific age, we can only speculate that individual variation in the fate of the bodies could have strongly influenced the results. No previous results on the effect of large herbivore carcasses on the Ca content of soil are available for comparison, but it is likely that Ca is mainly released by the bones, and our results suggest that its cycling is slower than that of other nutrients.

The variation in soil N concentration was mainly influenced by the age of the carcass. The fact that the concentration of NO_3^- in the soil was higher only at the 1-year-old carcass site might suggest that cycling of N is rapid. This is not surprising if we consider that plant growth in temperate forests is most frequently limited by N availability (Aber et al. 1998). Towne (2000) also found that inorganic N levels at carcass sites were higher in the inner 50 cm than in soil at a distance of 2 m for only up to 2 years after the death of the animal. Thus, the observed differential response in soil nutrients may be related to their specific turnover rates. Our results suggest a certain effect of carcasses on the soil concentration of K and P, although this effect was not recorded at all carcasses. We detected the presence of a gradient in K and P at the 3- and 5-year-old carcasses and at the 5-, 6- and 7-year-old carcasses, respectively. Whether the reason for this difference between carcasses was due to specific nutrient turnover rate or to the characteristic of the sites themselves is not clear. Towne (2000) did not find any difference in the concentration of K and organic

matter levels between the centre of the carcasses and the surrounding prairie 5 years after death.

The characteristics of the soil at the carcass location may also contribute to the lack of a consistent pattern in the soil nutrient response as well as in the pH. Our result of a higher pH at the centre of the carcass was opposite to the findings by Towne (2000) in a prairie habitat. However, our pattern was similar to that found for experimental pig graves, where the highest pH values of the graves' soil coincided with the release of NH_4^+ (Hopkins et al. 2000). We have to emphasize that our sample size is small and that there is also an almost total overlap between the variable 'age' and 'site'. The effect of site was almost always significant since the soil and vegetation were sampled in different areas of the BPF with different average soil nutrient concentrations. The types of soil and forest types present in the BPF are very diverse (Kwiatkowski 1994). However, if the effect of a bison carcass was difficult to detect, the impact of smaller carcasses, which are more easily dragged around by predators and scavengers, might be even more difficult to measure.

The fact that the plant community composition and abundance did not differ between carcass and control sites and the weak response of the nutrient concentration in the vegetation along the gradient may suggest that nutrients are not a limiting factor in the nutrient-rich temperate forests. Other limiting factors, such as light exposure, might affect the ability of plants to colonize the carcass site. This is in contrast to the Arctic tundra where nutrient availability is low, and carcasses do have a dramatic effect on vegetation (Danell et al. 2002).

With the exception of Na, the concentration of nutrients in the sampled vegetation was constant over time and space in the BPF. This absence of a clear pattern in the soil and vegetation concentration of some

nutrients at the carcass sites and surroundings may be due to several factors. First, the activities of scavengers may greatly influence the influx of nutrients from carcasses into the surrounding soil and, subsequently, into the vegetation. BPF has a very complex and rich community of large predators and scavengers that efficiently consume most available carrion and often move the carcass or its parts (Selva et al. 2003, 2005). This affects the nutrient distribution along the gradient, as the centre of the bison carcass often changed position due to dragging by wolves and the carcass remains were usually scattered (Selva et al. 2003). Thus, scavengers in the BPF determine to a great extent the length of time the carcasses are releasing nutrients into the soil before they are totally consumed. Our results suggest that a large proportion of the carcass-derived nutrients are recycled via scavenging and therefore transferred to distant areas. They are also indicative of the important role of scavengers in spreading such nutrients over wide areas. Scavenging was unrecorded and may have been of little importance in previous studies in the prairie and tundra (Towne 2000; Danell et al. 2002), a fact that may contribute to the clearer gradient in nutrient concentration observed. Carcasses are mainly available in winter, when they are almost fully consumed by vertebrate scavengers (Selva 2004). Only at warm temperatures does decomposition become important (DeVault et al. 2004; Selva et al. 2005), thus allowing leachates to concentrate in the soil (Towne 2000).

We conclude that the effect of large herbivore carcasses on the nutrient concentrations of soil and plants is less evident in the temperate forest than in more homogeneous habitats, such as tundra and prairie. In natural temperate forests the intense activity of scavengers leads to rapid nutrient cycling, and the synergistic influence of limiting factors might make it difficult to detect the impact of carcasses on soil and vegetation. This does not mean that large herbivores have a smaller impact on the nutrient cycling and plants, but simply that the interaction between nutrient availability and other limiting factors is more complex and patchy.

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