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RESEARCH ARTICLE

Rewilding Europe's large grazer community: how functionally diverse are the diets of European bison, cattle, and horses?

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Trophic rewilding is the introduction of species to restore top–down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems. A core example of trophic rewilding is the restoration of large mammalian grazer communities to restore or maintain biodiverse open to half-open landscapes. Across Europe, cattle and horse breeds are being introduced as substitutes of the extinct aurochs (*Bos primigenius*) and tarpan (*Equus ferus*). More recently, European bison (*Bison bonasus*) is being introduced because it is supposed to fill a niche that pure grazers such as cattle and horses leave empty, especially in terms of reducing woody encroachment. But how functionally diverse are the diets of these three species? We investigated this question in the Kraansvlak pilot; a trophic rewilding project in the Netherlands where European bison, horses, and cattle have been introduced in spatially heterogeneous landscapes of forest, shrub land, and grassland. We present 4 years of data from direct observations on the diet use of all three species. Whereas cattle and bison included a significant proportion of woody plants in their diet throughout the year, horses strictly grazed. However, cattle and bison differed clearly in terms of the woody plant part they used (bark vs. twigs), and we discuss how this may affect the way they influence vegetation structure. Finally, we discuss the implications of our study for the increasing number of trophic rewilding initiatives in Europe.

Key words: ***Bison bonasus*, *Bos taurus*, *Equus ferus*, grazing, refugee species concept, substitute species, woody encroachment**

Implications for Practice

- Trophic rewilding with European bison, horses, and cattle can work without supplementary feeding, also in relatively small nature reserves.
- The three species found sufficient natural food sources throughout all seasons and their diets consisted predominately of grass (≥ 80–90% of diet).
- European bison and cattle, but not horses, included a significant proportion of woody plants in their diet (20%) throughout the year.
- In winter and early spring, European bison debarked trees, whereas cattle browsed twigs, which suggests that they may have a different impact on woody communities.
- The foraging behavior of European bison did not reflect that of a strict forest species, but rather that of a species that prefers a mixture of grassland and wooded habitats.

Introduction

In many parts of the world, the concept of rewilding (Reardon 2014; Svenning et al. 2016) is increasingly influencing conservation and land-use agendas (Bauer et al. 2009; Navarro & Pereira 2012; Ceauşu et al. 2015; Pereira & Navarro 2015; Jepson 2016). Navarro and Pereira (2012) defined rewilding as "passive management of ecological succession with the goal of restoring natural ecosystem processes and reducing human control of landscapes." More recently, Svenning et al. (2016) introduced the concept of *trophic rewilding* and defined it as "species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems." A key example of trophic rewilding is the restoration of the process of grazing by large mammalian herbivores (Naundrup & Svenning 2015) to restore or maintain open to half-open, structurally diverse, landscapes (Olff et al. 1999; Smit & Putman 2010). Woody encroachment of such landscapes is seen as a serious threat to biodiversity (Ostermann 1998; Cremene et al. 2005; Henle et al. 2008; Bergmeier et al. 2010). Consequently, free-ranging cattle and horse breeds are being introduced across Europe and elsewhere in the context of ecological restoration (Van Wieren 1995; Wallis De Vries et al. 1998; Finck et al. 2002; Smit et al. 2015).

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Following the rewilding philosophy, these introductions must be seen in the light of the relatively recent extinctions of Europe's wild large grazers; the aurochs (*Bos primigenius*) and the tarpan or Eurasian wild horse (*Equus ferus*) (Naundrup & Svenning 2015). Both species were originally distributed across Europe and further east into Eurasia but the last aurochs died in Jaktorów forest in Poland in 1627 (Szafer 1968) while tarpan survived until the first decades of the twentieth century (Vereshchagin & Baryshnikov 1993). Although there is an ongoing debate about the historical importance of these large grazers for creating and maintaining more open landscapes in northwestern Europe (Svenning 2002), recent evidence suggests that they may have played this role during the last interglacial, 132,000–110,000 years BP, before they were hunted to extinction or functionally insignificant densities by humans (Sandom et al. 2014). Aurochs and tarpan, however, survived in their domesticated forms. Domestic cattle and horses are, therefore, increasingly seen as functional equivalents, or ecological replacements (Griffiths et al. 2010; Svenning et al. 2016), of aurochs and tarpan (Naundrup & Svenning 2015), and there are now more and more efforts focused on rewilding horses (Linnartz & Meissner 2014) and cattle (Vermeulen 2015). However, when thinking about rewilding Europe's large grazer community, one species should not be ignored, the European bison (*Bison bonasus*). Although European bison went extinct in the wild in 1927, it was reintroduced in the wild in Białowieża forest, Poland, in 1952 following a successful breeding program in zoos (Pucek 2004). Since then, the population has grown considerably and European bison have been reintroduced in several areas in mostly Eastern Europe, but increasingly in western and southern Europe as well (Kerley et al. 2012). Apart from species conservation, several of the recent introductions are implemented as trophic rewilding initiatives; e.g., in Denmark (Brandtberg & Dabelsteen 2013) and Spain (Burton 2011). The suggestion is that bison, as a mixed feeder from forested environments (Hofmann 1989; Krasińska & Krasiński 2007), fills a niche that pure grazers such as cattle and horses leave empty, especially in terms of reducing woody encroachment.

The classic view of European bison as a typical forest species was recently challenged by Kerley et al. (2012), who suggested that bison is a refugee species that evolved on open steppe habitat and was pushed into refuge forest areas through anthropogenic factors (see also Cromsigt et al. 2012). A recent isotope-based study provided empirical support for the refugee hypothesis and showed that, in contrast to moose, early Holocene bison used open habitats (Bocherens et al. 2015). Unfortunately, our knowledge of extant European bison is predominantly based on bison living in forested areas in which they are fed supplemental hay during winter time (Kowalczyk et al. 2011). Until this date, there is a lack of studies looking into the foraging behavior of European bison that do not receive supplemental feeding and that live in landscapes that are not fully dominated by forest. In addition, we are not aware of any studies that directly compare the foraging behavior of European bison, cattle, and horses in the same habitat. This begs the question, how functionally diverse are the diets of these three species? This is a crucial question since there is now an increasing push toward restoring herbivore communities that include all three European large grazers; cattle, horses, and European bison. The main argument for restoring these communities is the functional complementarity of the three species; that is, that cattle, horses, and bison differ in their diet use and thus impacts on the landscape (see e.g., Van de Vlasakker 2014). Unfortunately, we currently lack strong empirical evidence to support such an argument.

We present some of the first results of a unique trophic rewilding project in the Netherlands (*the Kraansvlak pilot*), where European bison, horses, and cattle have been introduced in a spatially heterogeneous landscape of forest, shrub land, and grassland. Within the confines of the fenced reserves, all three species are free-ranging year-round and do not receive any supplemental feeding, even during winter. In contrast to many other rewilding initiatives (Svenning et al. 2016), the project has had intense scientific monitoring since its start in 2007. Here, we present data on the diet composition of all three species, collected over a 4-year period through a large number of observations of individual bites.

Methods

Study Area

Our study took place between 2008 and 2012 in National Park Zuid-Kennemerland (NPZK), a coastal dune reserve in the Netherlands between IJmuiden and Zandvoort. The area experiences a temperate maritime seasonal climate. Average monthly temperature is 3–4°C in January and 17–18°C in July, and less than 10 days per year temperatures drop below 0°C for the whole 24 hours (average during 1981–2010, http://www.klimaatatlas.nl). Average annual precipitation is around 850–900 mm, and during an average winter, the ground is covered by snow for less than 10 days per year (average during 1981–2010, http://www.klimaatatlas.nl). We focused on two areas within the NPZK that are separated by a main road; the Kennemerduinen area (52°25′1.41″N; 4°34′54.53″E), consisting of circa 2,069 ha, and the Kraansvlak area (52°23′17.03″N; 4°34′13.11″E), consisting of around 220 ha at the time of this study. The Kennemerduinen is accessible for recreational use though it is surrounded by a fence to keep cattle and horses in, whereas Kraansvlak is fenced out and at the time of study was not open for the public except for guided excursions.

Both areas are characterized by large variation in vegetation types; open sandy dune areas, dry and wet grasslands, both deciduous and coniferous forest patches, and shrub land characterized by a continuous grass layer and shrubs of several woody species (particularly, spindle tree *Euonymus europaeus*, sea-buckthorn *Hippophae rhamnoides*, hawthorn *Crataegus monogyna*, and creeping willow *Salix repens*). In both areas, permanent water bodies are present in the form of small dune lakes. The areas are similar in the overall proportions, and thus availability, of main vegetation types (Table 1). Due to the heterogeneity of the landscape, grasses and forbs as well as woody plants are amply available across both areas.

Table 1. Main habitat types and their percent cover for the Kraansvlak (from Everts et al. 2006) and Kennemerduinen (from Everts et al. 2005, 2006).

Habitat type	*Percent cover Kraansvlak*	*Percent cover Kennemerduinen*
Open sand	3	3
Water bodies and wetland	2	3
Grassland	53	33
Shrub land	26	29
Deciduous forest	10	23
Coniferous forest	6	9
Total Ha	220	2069

Study Animals

During the time of study, approximately 80 Highland cattle (Scottish cattle breed, hereafter: cattle) inhabited the Kennemerduinen area along with circa 30 Koniks (Polish primitive horses) and 30 Shetland ponies (see Table 2 for exact numbers). The cattle wander around in the area in several different groups, which are not constant in number and composition of individuals. Most individuals were introduced in March 2005, and at the end of that year every bull was sterilized, thus calves were born only for one reproductive season (P.W.N. Ruud Maaskant 2017, personal communication). Before 2007, Highland cattle and Konik horses grazed in the Kraansvlak, but these were removed before the start of the bison project. In April 2007, the first three bison arrived to Kraansvlak (one adult male and two adult females) from Pszczyna (male) and Białowieża (the females) forests, Poland. In March 2008, another three individuals from Białowieża were introduced (two adult females and one female calf). Between 2009 and the end of the study period (spring 2012), the herd increased to 16 bison due to natural growth. In October 2009, five Konik horses (hereafter: horses) were reintroduced to the area (four females and one male) and this group increased to 14 horses at the end of the study period. In both Kraansvlak (European bison and horses) and Kennemerduinen (cattle and horses) the animals select their diet from available natural food sources throughout the year. Supplementary feeding has not occurred in the areas since the animals were introduced. Management has been limited to regular non-invasive veterinary controls (visual inspections) to monitor welfare and health status and occasional sedation of individuals for specific veterinarian checks or fitting of GPS collars. Besides aforementioned large herbivores, fallow deer and roe deer as well as rabbits are present in both areas and they are able to move in and out of the fenced areas.

Behavioral Observations

We observed the foraging behavior of the cattle in the Kennemerduinen, whereas the European bison and horses were observed in Kraansvlak. Observations were made from after dawn until well before dusk to ensure enough daylight to observe foraging animals through binoculars. The length of observation days thus differed among seasons, varying with daylight length, but did not differ among species. Cattle were observed from February 2008 to November 2011 by 14 different observers during 106 observation days (total of 562 observed feeding bouts of which 167 in autumn, 179 in spring, 129 in summer, and 87 in winter). The foraging behavior of horses was recorded from February 2010 to May 2012 by eight different observers during 81 observation days (403 feeding bouts: 38 in autumn, 181 in spring, 62 in summer, and 122 in winter). European bison were studied from February 2008 to June 2012 by 18 different observers during 169 observation days (1,100 feeding bouts: 371 in autumn, 418 in spring, 130 in summer, and 181 in winter). To limit observer biases, we ensured that the same observer always observed more than one species. Observations on the three species were distributed across all months of all years and were not highly skewed toward a certain species or time period or highly clumped in very small time intervals (see Table S1, Supporting Information). To find animals we used GPS-collar data of each species that fixed the location of the respective herd once per hour. Based on the last known location, we localized the animals and then approached them on foot as closely as possible, while keeping a minimum of 50 m distance to avoid influencing the behavior of the animals. The terrain of both areas (undulating dune hills with regular woody cover) allowed us to observe animals without noticeably disturbing their feeding behavior. We used the same bite-step protocol to quantify foraging behavior of all three species. At the start of each observation, a random, but well visible, foraging individual was chosen, and we limited ourselves to adult individuals. We defined an animal as foraging when the animal was clearly taking bites from the vegetation. We used a portable voice recorder to continuously record each bite and step taken by the animal following Underwood (1983). For each bite, we recorded the food type that dominated that bite according to five broad dietary classes; grasses, forbs, woody plants, roots (of grasses, sedges, or rushes), or lake shore plants (sedges and rushes). For each bite of a woody plant, we also recorded the plant part (bark, twig, fruit, or leaf) and the species of woody plant. We defined a bark bite as debarking of the main stem or large branches (so not twigs). Bark bites were thus never mixed with bites from the other plant parts. Fruit bites were mostly acorns (approximately 70% of fruit bites) and the remainder of fruit bites were berries from shrubs such as hawthorn. In all these cases, animals clearly selected the fruit but could also have taken in some twigs or leaves. Leaf bites were defined as an animal that was stripping or feeding on leaves, although the same bite could also include twig but not fruit. Twig bites were defined as animals that were browsing on twigs that had no leaves. The observation ended when the selected individual did not forage for more than 2 minutes or if its behavior was no longer visible. Then, a new observation started on the next visible individual.

Data Analysis

Our data were collected by a large number of observers that each performed observations during a relatively short time (a few months per observer). During this short time, many observers did not learn to recognize the different individuals in the herd, particularly when the herd size had significantly increased. As

Table 2. Number of individuals per large grazer species, per 31 December of each year, for both study areas: Kraansvlak (bison area) and Kennemerduinen (cattle area). These numbers are based on frequent monitoring of the herds by the managing authority. Besides the numbers, the total biomass of large grazers is given per year and per study area as the number of animals multiplied with individual body mass summed over all species in the area. For the biomass density we used as average female body mass 350 kg for Konik horse, 450 kg for bison and cattle, and 200 kg for Shetland pony and divided those with 220 and 2,069 ha for Kraansvlak and Kennemerduinen, respectively. Biomass density estimates are maximum estimates and do not take into account individual variation in body mass and the fact that several of the individuals in the herds were calves/foals or subadults.

	2008	*2009*	*2010*	*2011*	*2012*
Kraansvlak					
European bison	6	10	14	16	16
Konik horse	0	5	8	11	14
Biomass density (kg/ha)	~12	~28	~41	~50	~55
Kennemerduinen					
Highland cattle	80	80	80	80	79
Konik horse	29	29	29	29	33
Shetland pony	30	28	27	27	25
Biomass density (kg/ha)	~25	~25	~25	~25	~25

a result, there was a large number of observations that we could not relate to known individuals, and we could thus not use individuals as sample units in our analysis. Therefore, we choose a different approach to analyze the dataset. We summed all bites over all recorded individuals per observer during one observation day, grouped per diet category, and treated observers as independent sampling units. To control for temporal autocorrelation, we used a mixed-effect model where we nested season, species, and observer in observation date and included this as a random effect (Pinheiro & Bates 2000). As response variables, we calculated the proportion of bites for the different dietary classes per observation day, as explained above, for each herbivore species separately (90% of these days consisted of at least 150 bites). We performed an arcsine square root transformation on all the proportion data before further analysis. We used animal species, season, and the interaction between the two as fixed effects. Seasons were based on Dutch meteorological standards; spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). We used R version 3.2.2 for all analyses (R Development Core Team 2015), and the function lme from the nlme package for the mixed-effect models.

Results

All three large herbivore species predominantly fed on grasses and the proportion of grass bites did not differ among species ($F_{2,20} = 0.42$, $p = 0.67$, Fig. 1) for any of the seasons (species × season; $F_{6,20} = 0.62$, $p = 0.99$). The proportion of woody bites varied among species ($F_{2,20} = 14.4$, $p < 0.001$) and this pattern was consistent across seasons (species × season; $F_{6,20} = 0.11$, $p = 0.99$). While both cattle and European bison had similar proportions of woody plant bites in their diet of around 20%, horses differed from both bison and cattle and had close to 0% woody plant bites in their diet (Fig. 1). Herbivore species did not differ in the proportion of forb bites ($F_{2,20} = 0.49$, $p = 0.62$) and this was consistent among seasons (species × season; $F_{6,20} = 0.21$, $p = 0.97$). Lake shore plants were only eaten by the horses during spring and summer, with no bites during autumn and winter while cattle and bison hardly foraged upon this food type at all (Fig. 1). Only the horses were observed eating roots and only during spring and winter (Fig. 1). Bison and cattle were not observed eating roots at all.

We analyzed the woody bites in more detail, to test if the different herbivore species selected for different parts of the woody plants. Because horses hardly foraged upon woody species during our study, we excluded them from this analysis. Cattle and European bison had equal proportions of leaf bites ($F_{1,13} = 0.31$, $p = 0.59$) and this proportion varied among seasons ($F_{3,12} = 21.99$, $p < 0.001$) in the same way for both species (species × season; $F_{3,12} = 0.07$, $p = 0.98$). For both cattle and bison, almost 100% of the woody plant bites during summer consisted of leaves, with 60–80% during autumn, 30–40% during spring, and less than 10% in winter (Fig. 2). Both species only foraged upon fruits during autumn and in similar proportions ($F_{1,13} = 0.005$, $p = 0.95$). However, cattle and bison differed in their use of twigs ($F_{1,13} = 18.4$, $p < 0.01$) and bark ($F_{1,13} = 16.1$, $p < 0.01$), and these differences were consistent among seasons (species × season interaction for twigs: $F_{3,12} = 3.2$, $p = 0.06$ and bark: $F_{3,12} = 1.44$, $p = 0.28$). Cattle had considerably more bites of twigs in their diet than European bison. During winter and spring, cattle had 50–70% bites of twigs in their diet versus 20–30% for bison (Fig. 2), whereas during summer and autumn, the proportion of twig bites was low for both species (<10%) (season; $F_{3,12} = 15.8$, $p < 0.001$). In contrast, European bison had a much higher proportion of bark bites (>60% during winter) than cattle (never >20% of bites) (Fig. 2). Debarking strongly depended on season ($F_{3,12} = 7.2$, $p < 0.01$) with most debarking in winter, followed by spring and autumn, and almost no debarking in summer.

Highland cattle and European bison were similar in terms of the woody plant species they foraged upon (Table 3). Four species made up greater than 85% of the woody bites by European bison (*Euonymus europaeus*, *Quercus robur*, *Salix repens* [perhaps some *cinerea*], and *Crataegus monogyna*). Highland cattle included the same four species supplemented with *Prunus* spp. (mostly *serotina*). Depending on the woody species, different plant parts were preferred (Table 3). Both cattle and bison

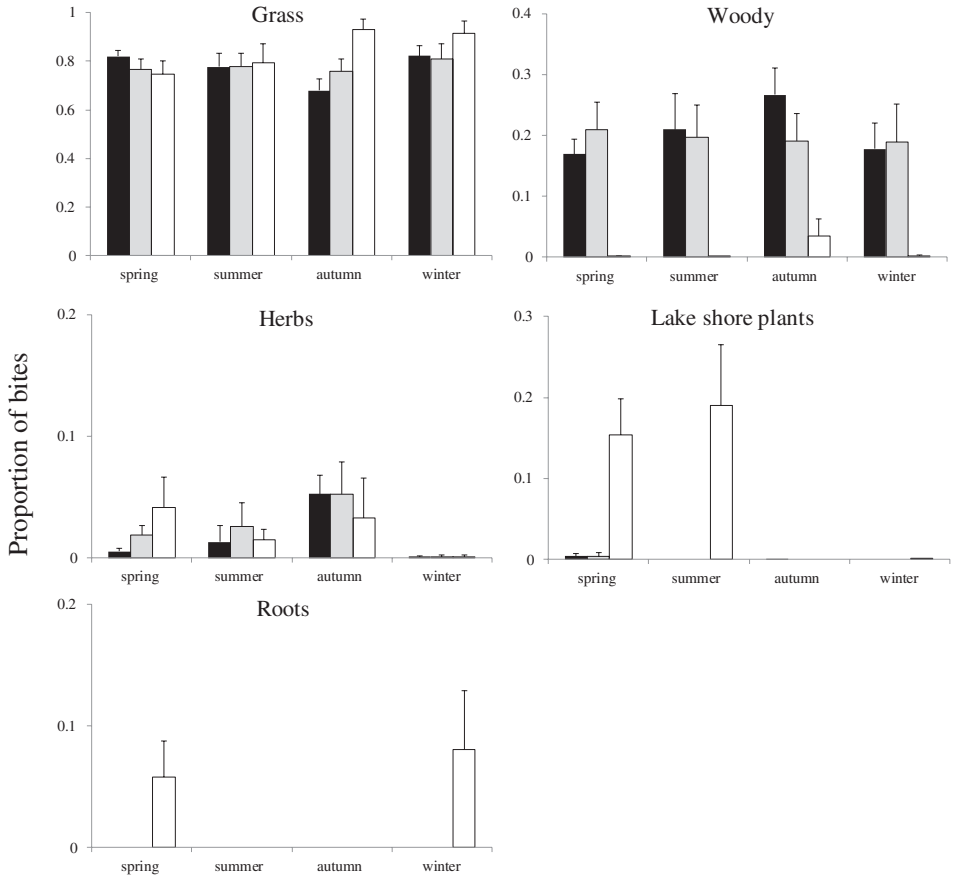

Figure 1. Average proportion (+SE) of bites of different food types in the diet of European bison (black bars), cattle (gray bars), and horse (white bars) during the four seasons. Seasons were defined as spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). Please note different scaling of *y*-axes for the different food types. Consumed lake shore plants were predominately sedges and rushes.

foraged upon *Crataegus monogyna*, *Prunus* spp., and *Salix repens* for their leaves, although cattle also used *Salix* for its twigs. In contrast, *Euonymus* was mostly chosen for its bark by both herbivores. European bison selected *Quercus robur* for its acorns (>80% of bites), whereas cattle consumed acorns but also included a fair proportion of *Quercus robur* twigs (28%) in their meals.

Discussion

We have provided some of the first empirical data concerning the diets of Europe's three largest grazers, European bison, cattle, and horses, living under similar conditions in a heterogeneous landscape without supplementary feeding. All three species predominately foraged on grasses throughout the year (≥ 80% of diet). Whereas the two bovids, cattle and bison, included a significant proportion of woody plants in their diet (20%) during all seasons, horses did not but supplemented their grass diet with sedges and herbs. The two bovids differed clearly in terms of the woody plant parts they used (bark vs. twigs) and we speculate below how this may affect the way they influence vegetation structure. Our study thus provides some first empirical data on the differences in diet use among Europe's largest grazers, which can inform trophic rewilding initiatives that focus on introducing the full complement of these species.

Our results confirmed other studies that showed that cattle include a much larger proportion of woody species in their diet than horses (e.g. Cosyns et al. 2001; Vulink et al. 2001; Menard et al. 2002; Lamoot et al. 2005). Vulink et al. (2001) suggested that this is due to the prevalence of secondary plant compounds in certain woody species which ruminants, in contrast to the hindgut fermenting horses, are able to detoxify to some extent in their fore stomach (Vulink et al. 2001). Horses have been found to use woody plants and regularly debark in other areas though (e.g., Kuiters et al. 2006). Such contrasting findings may have to do with differences in food availability among areas. In our study areas, grasses and sedges/rushes are amply available throughout the year.

Both cattle and European bison in our study would be classified as grazers with circa 80% grass bites in their diet during all seasons, or perhaps as grazers tending toward the intermediate feeding type, similar to the position Hofmann (1989) gave bison in his original feeding type classification. Our results suggest that, in terms of proportion grass versus woody intake, bison and cattle should be classified as having similar feeding

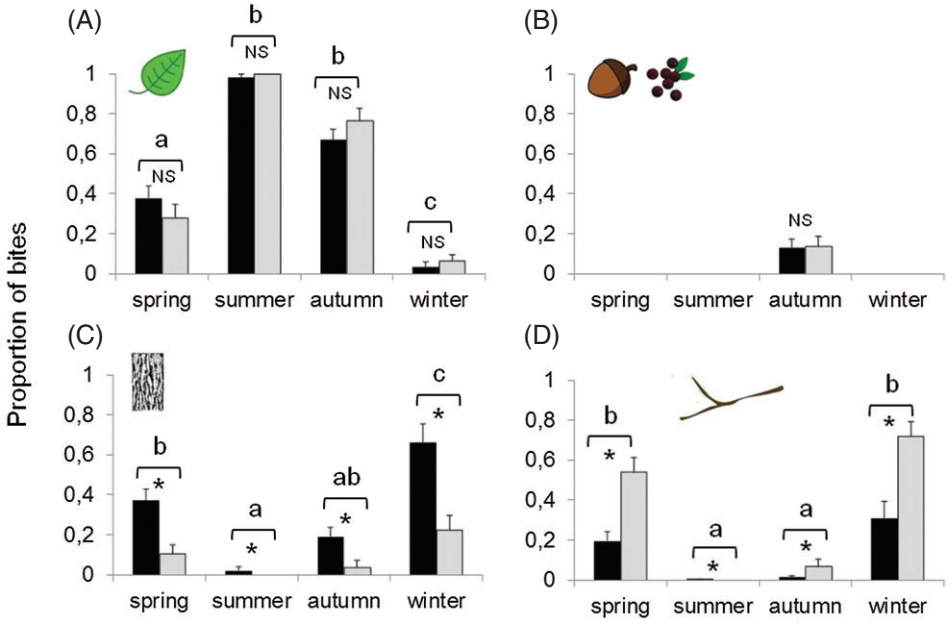

Figure 2. Average proportion (+SE) of bites of different woody plant parts in the diet of European bison (black bars) and cattle (gray bars) per season. Seasons were defined as follows: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). Panels show leaves (A), fruits (B), bark (C), and twigs (D). Letters above brackets show pairwise comparison results for season, where different letters indicate significant differences ($p < 0.05$). NS (not significant) or asterisk ($p < 0.05$) under the bracket indicates whether proportion of bites was significantly different between European bison and cattle.

Table 3. Plant species making up greater than 80% of woody bites selected by European bison and cattle, with plant parts per woody species indicated. Highest percentage per grazer/plant species combination in bold.

Plant Species	*Herbivore*	*% of Woody Bites*	*% Bark*	*% Twig*	*% Leaf*	*% Fruit*
Euonymus europaeus	European bison	41	**81**	8	11	0
	Highland cattle	13	**77**	12	11	0
Quercus robur	European bison	19	10	5	3	**82**
	Highland cattle	15	5	28	8	**59**
Salix repens (possibly some *cinerea*)	European bison	15	0	18	**72**	0
	Highland cattle	21	0	**55**	45	0
Crataegus monogyna	European bison	14	8	3	**85**	4
	Highland cattle	10	0	9	**91**	0
Prunus serotina and/or *padus*	European bison	<1	0	0	**100**	0
	Highland cattle	26	0	4.5	**95**	0.5
Total number of bites	European bison	19,609				
	Highland cattle	16,439				

strategies, meaning that cattle should move toward the position of bison in the original figure by Hofmann (1989). Previous studies on bison diet from Białowieża forest, Poland, also indicated a diet dominated by grasses and other herbaceous material in summer and winter, despite the fact that this is a forest environment (e.g. Borowski et al. 1967; Borowski & Kossak 1972; Gębczyńska & Krasińska 1972; Gębczyńska et al. 1991). However, this predominance of grass in winter diet in Białowieża is to a large extent influenced by supplementary feeding. Kowalczyk et al. (2011) showed that the proportion of woody plants increases strongly for bison that hardly visit feeding sites. An extensive use of woody plants in winter may thus be an effect of habitat with limited grass availability. In Kraansvlak, grass is available year-round. Moreover, in many areas in Eastern Europe, the herbaceous layer may be covered by snow during several months a year. However, snow in itself does not limit access to grass by American *Bison bison bison*, which craters to access grass (e.g., Wallace et al. 1995). Only snow depths of greater than 30 cm seem to start influencing bison foraging behavior (Fortin et al. 2003). We have observed similar cratering behavior by bison in the Kraansvlak, sweeping away snow with their muzzles and hooves (E, Rodriguez & Y. Kemp 2008–2012, personal observations).

Both bovids used the same woody species and the use of species depended on plant part; *Euonymus europaeus* was used for bark, *Crataegus* spp. and *Prunus* spp. for leaves, and *Salix*

spp. for leaves and twigs. While cattle and European bison were very similar in terms of the proportion of woody plants in their diet, perhaps one of the most striking results of our study was that the two bovid species used different woody plant parts. In short, during late autumn, winter, and early spring bison stripped bark whereas cattle browsed twigs. We speculate that this difference in foraging behavior may result in a different impact on the vegetation. Bark stripping, by limiting phloem transport, arguably has considerably more impact on plant survival than browsing on twigs, although very few studies have looked at this (but see Scogings & Macanda 2005). We thus predict that European bison in Kraansvlak should have a stronger negative effect on woody plant survival than cattle in the Kennemerduinen. Oquiñena-Valluerca (2011) compared high-resolution (approximately 20 cm pixels) aerial photos from 2003 (before bison introduction) with photos from 2009 (2 years after bison introduction) for intensely and less intensely used areas in the Kraansvlak based on hourly GPS fixes of the bison herd. While on average woody cover increased with 8% in the Kraansvlak between 2003 and 2009, it decreased with 4% in areas that were intensely used by bison (40% isopleth of the Kernel utilization distribution). This analysis suggests that bison can halt or even reverse woody encroachment in areas that they use intensely. Unfortunately, we lack such an analysis of aerial photos from the cattle area. A preliminary analysis of permanent vegetation transects suggests that changes in woody plant density and viability were in fact relatively similar between the bison and cattle area (Valdés-Correcher et al. in review). Direct comparison of impact on the woody plant community between the bison and cattle areas is somewhat limited, however, by the fact that the two areas do not only differ in bison versus cattle presence but also in average herbivore biomass density (see Table 2).

As already highlighted in our above discussion of the horse diet, it is important to recognize that diet use strongly depends on availability of plant species. The comparison of diet use among herbivore species depends on the assumption that species have access to the same food sources. As horse and bison co-occurred in the same area and had access to the exact same food sources, this did not affect the comparison of food utilization between these two species. However, bison and cattle occurred in different, though environmentally very similar, areas. We thus have to be careful with using our results to draw general conclusions about differences in diet use between cattle and European bison. In terms of the plant functional groups (grass, woody, etc.) and woody plant parts, we believe that food availability was similar between bison and cattle areas (see Table 1 for similarity in habitat availability). However, there were some differences in the availability of certain woody species. For example, the fact that cattle used more *Prunus* than bison probably reflects a lower availability of this species in the Kraansvlak than in the Kennemerduinen (*personal observations*). We cannot fully exclude that our finding that bison debarked more than cattle was partly due to differences in availability of certain woody species between areas instead of intrinsic species differences. As European bison and cattle did not occur in the same area during our study period they were not in direct competition. It is well-known that diets might diverge more when species can directly interact (see e.g. Du Toit & Olff 2014). Our observation that the diets of cattle and bison were generally quite similar may be due to this lack of competition. Mid-2016, Highland cattle were introduced to the Kraansvlak to live alongside the European bison and Konik horses and we are continuing our observations of foraging behavior. Soon we will thus be able to test if cattle and bison diets diverge more when coexisting in the same area.

For several of the reasons discussed above, one should be careful with generalizing the differences in foraging ecology that we found among the three large grazers. However, we have provided some of the very first empirical data on the foraging ecology of European bison, cattle, and horses under similar conditions in a trophic rewilding context. Such data are important for rewilding initiatives that aim at restoring grazing as an ecological process by introducing multispecies large grazer assemblages (Navarro & Pereira 2012; Svenning et al. 2016). Even more so, however, we would like to urge others to start similar trophic rewilding experiments, using the Kraansvlak pilot and methodologies as inspiration (Jepson 2016). Only with a sufficient number of similar studies, we can perform the urgently needed meta-analyses that could lead to more generally applicable knowledge about the foraging ecology, and impact, of Europe's largest grazers.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Distribution of the number of observations per herbivore species across each month and year.

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