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ORIGINAL PAPER

Comparing the impact of a grazing regime with European bison versus one with free-ranging cattle on coastal dune vegetation in the Netherlands

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Abstract

Woody plant encroachment has increased across the globe and threatens biodiversity associated with open habitats. In order to prevent or reduce woody encroachment, conservation managers across Europe introduce large mammalian herbivores. While up to recently, managers were mostly using free-ranging domestic cattle and horses for this, there is an increasing interest in the use of European bison for nature management. However, we lack studies that compare the impact of these different grazers on vegetation. We report results from a unique grazing pilot in the National Park Zuid-Kennemerland, a heterogeneous coastal dune landscape in the Netherlands, where European bison, horses, and cattle were introduced to reverse the encroachment of grass and shrub species. We present results of an 8-year study on the development of woody and grassy vegetation on fixed transects in three different grazing areas within the national park; one area with European bison and horses, one area with cattle and horses, and one area where these large grazers were excluded. In all three areas, rabbit, fallow deer, and roe deer were present. Over time, we observed strong reductions in the vitality of several woody species, such as spindle tree, and this decline was similar across all areas. Grass height and cover also declined and the proportion of herbs increased in all three grazing areas in similar ways. However, the type of herbivore use (debarking, foraging on buds, branches) of several woody species differed significantly among areas. For instance, maple tree was only debarked in the E. bison area, while hawthorn branches were eaten significantly more in the cattle than in the bison area. Due to differences in herbivore densities among areas, it was difficult to draw strong conclusions on how the different herbivore species differed in their impact, but, importantly, we found that grazing regimes with bison can lead to as strong effects on vegetation structure and composition as grazing regimes with cattle. This is an important result since certain conditions, such as legal aspects, may motivate managers to introduce a wild large grazer rather than a domesticated one.

Keywords European bison · Grazing regime · The Netherlands · Woody encroachment

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Introduction

Over the past few decades, woody plant encroachment has increased across the globe (Van Auken 2000; Archer et al. 2001). This succession towards vegetation dominated by shrubs and trees threatens biodiversity associated with open habitats (Bergmeier et al. 2010). In Europe, an important driver of woody encroachment is farm abandonment and the disappearance of large grazing herbivore species from the landscape (MacDonald et al. 2000; Fuchs et al. 2013). Large mammalian herbivores may affect woody vegetation, resulting in mosaics of woody and grassy open habitats through consumption and direct physical impacts such as trampling (Olff et al. 1999; Smit and Putman 2010). Therefore, to counteract woody encroachment, nature managers are increasingly

introducing large herbivores in European ecosystems to restore the conditions for species of open habitats (Milchunas et al. 1988; Kooijman and Smit 2001; Smit et al. 2015).

Up to recently, introductions of large mammalian herbivores for nature management purposes have mostly focused on cattle (*Bos taurus* L.) and horses (*Equus ferus caballus* L.) (Rook et al. 2004) as functional equivalents of the extinct aurochs (*Bos primigenius*) and Tarpan or Eurasian wild horse (*Equus ferus*) (Naundrup and Svenning 2015). However, the extant European large grazer community includes an additional species, the European bison (*Bison bonasus* L.). This species went extinct in the wild in 1927, but thanks to a dedicated breeding program, the first bison could be released back into the wild in the 1950s (Pucek et al. 2004). Since then bison have been re-introduced, mainly in forested areas across Europe (Kerley et al. 2012), to improve the species conservation status. More recent initiatives also introduce bison for its ecological role, assuming that bison functionally complements cattle and horse (Cromsigt et al. 2017). In contrast to these grazers, European bison has been hypothesized to be more of an intermediate feeder (Hofmann 1989), which has been confirmed through teeth microwear analyses (Merceron et al. 2014) and observations of bison frequently foraging on woody species during winter (Borowski et al. 1967; Gębczyńska and Krasińska 1972; Kowalczyk et al. 1976, 2011). Some studies have shown that European bison is able to digest lignin better than cattle, suggesting that they could include a bigger proportion of woody plants in their diet than cattle (Gębczyńska and Krasińska 1972). As a result, some of the recent reintroduction initiatives assume that bison will be more effective in terms of reducing woody encroachment than cattle and horse (Cromsigt et al. 2015).

However, other studies suggest that European bison originally inhabited open or half-open grassy landscapes (Cromsigt et al. 2012; Kerley et al. 2012; Bocherens et al. 2015) and was pushed into more forested areas by anthropogenic pressures during the early Holocene as refuge habitat (Kerley et al. 2012). In fact, studies on current-day bison confirm that European bison, even when living in forested areas, select for open habitats (Kowalczyk et al. 2013; Wołoszyn-Gałęza et al. 2016). A recent study from the Kraansvlak area in the Netherlands showed that European bison had a similar diet use as cattle and horse, with at least 80% grass in the diet throughout the year, but also about 20% of woody plants in the case of bison and cattle (Cromsigt et al. 2017). Other work has also indicated a mixed diet of grass and woody plants (e.g., Merceron et al. 2014; Bocherens et al. 2015). Moreover, although cattle and horse are strict grazers according to Hofmann (1989), they may also feed extensively on woody species, sometimes leading to a reduction of tree and shrub cover (Everitt et al. 1981; Kuiters et al. 2006; Hedtcke et al. 2009; Popp and Scheibe 2013). Thus, although cattle and horse are traditionally seen as strict grazers and bison as an intermediate feeder (Hofmann 1989), there are strong suggestions that bison, cattle, and horse may be functionally more similar than previously assumed.

We report results from a unique grazing pilot in the National Park Zuid-Kennemerland, a heterogeneous coastal dune landscape in the Netherlands, where conservation managers introduced European bison and Highland cattle to reverse the encroachment of grass and shrub species in two adjacent, but separated, areas (Groen and Oosterbaan 2012). Both areas also host introduced Konik horses and none of these large grazers in these areas were supplementary fed, at any time of the year, throughout the study period. This design allowed us to compare the impact on the vegetation of a grazing regime with European bison with that of a grazing regime with cattle. We present results from 8 years of vegetation monitoring along fixed transects and specifically focused on (1) changes in the vitality of woody species, (2) changes in the proportion of trees used by herbivores, and (3) changes in grass and herb cover over time. We hypothesized that (1) the vitality of at least some woody species would decrease over time in both E. bison and cattle grazing areas (Powell and Box 1966; Kowalczyk et al. 2011), (2) the decrease in vitality of woody species would be stronger in the E. bison than cattle grazing area (Peden et al. 1974), and (3) grass cover and grass length would decline, while herb cover would increase over time, particularly in the cattle grazing area. Results of this study are of interest for European bison introduction projects elsewhere as well as for nature managers who are interested in using diverse sets of large herbivores for nature management purposes.

Material and methods

Study area

The National Park Zuid-Kennemerland (52° 26′ N, 04° 34 ′E) is a coastal dune area between Zandvoort and IJmuiden in the province of Noord-Holland and comprises 3800 ha. The area has a mean annual temperature of 7.8 °C, a mean annual rainfall of 766 mm, and its highest point above sea level is 45 m. This dune area is characterized by a heterogeneous landscape that includes deciduous and pine forest, dense and open shrubberies of different woody species (such as hawthorn (*Crataegus monogyna* Jacq.), sea-buckthorn (*Hippophae rhamnoides* L.), creeping willow (*Salix repens* L.), and spindle tree (*Euonymus europaeus* L.), open sandy areas as well as wet and dry grasslands (Cromsigt et al. 2007).

We monitored the vegetation on permanent transects in two areas inside the national park which were separated by a main road; Kennemerduinen (52° 25′ 1.41″ N; 4° 34′ 54.53″ E) that consists of 2069 ha and Kraansvlak (52°23′ 17.03″ N; 4° 34′ 13.11″ E) consisting of 438 ha (Fig. 1). The Kennemerduinen

Fig. 1 Map of the overall study area, the National Park Zuid-Kennemerland in the Netherlands, showing the location of the permanent vegetation transects; circles represent transects in the bison area, triangles transect in the cattle area, and squares transect in the grazing exclusion areas. The black line shows the boundaries of the Kraansvlak bison area; the gray line, the boundaries of the Kennemerduinen cattle area; the white lines, the boundaries of the grazing exclusion areas. The transects in the bison area were established in 2008 and 2009, except for one *Acer* transect that was established in 2013, while the transects in the cattle and grazing exclusion areas were established in 2011 and 2013, respectively

hosts introduced Highland cattle, Konik horses, and Shetland ponies (hereafter: cattle area), while European bison and Konik horses, but not cattle, were introduced to the Kraansvlak area (hereafter: bison area). Before the bison project started, 7 Konik horses and 15 Highland cattle inhabited the bison area, but these were removed a few months before European bison were introduced. In that sense, both cattle and bison areas presented similar conditions, in terms of historic grazing regimes, at the start of our study. Besides the introduced large grazers, rabbit (*Oryctolagus cuniculus* L.), fallow deer (*Dama dama* L.), and roe deer (*Capreolus capreolus* L.) occur in both areas and can move freely between them (see Table 1 for population estimates). The bison area, which is a fenced out part of Kraansvlak, consisted of 220 ha at the start of the vegetation monitoring in 2008 and was extended in 2012 to 280 ha and 2 years later to 330 ha. In 2007, the first 3 European bison were introduced in the bison area, followed by 3 more in 2008 (Smit et al. 2008). The herd increased to 24 individuals towards the end of the study period (2015) and decreased to 14 individuals during the last year due to translocations (2015–2016). In 2009, 5 Konik horses were introduced in the bison area and the group increased to 16 horses in 2014 but decreased to 4 during the last year of the study period (2016), again due to translocations. At the start of the study in 2008, 30 Shetland ponies, 29 Konik horses, and 80 Highland cattle occupied the cattle area. At the end of our study period, the number of Shetland ponies and Highland cattle had slowly declined to 22 and 65 individuals respectively, while the number of Konik horses had gradually increased to 43 individuals (Table 1). Besides the grazed areas, we monitored vegetation transects in areas within the cattle area where the large grazers were excluded but to which rabbit, fallow deer, and roe deer had access (hereafter: grazing exclusion areas). The average biomass density of rabbit, fallow deer, and roe deer in these grazing exclusion areas was fairly similar to the biomass density indicated for the cattle area (see Table 1) since exclusion areas were located within this area.

Transect layout

We monitored changes in vegetation structure and impact on individual trees on fixed line transects (Sutherland 2006). In 2008, we laid out 40 fixed transects in the initial 220-ha bison area distributed across four dominant habitat types (10 replicates per habitat type): pine forest, deciduous forest, sea-buckthorn shrubbery, and spindle tree shrubbery. In 2009, a further 10 transects were laid out in open grassland (Fig. 1). Transects were 50 m long and distributed randomly within each habitat type. Soon after the introduction of bison in 2007, we observed that European bison strongly targeted spindle trees. This triggered the question whether bison had a different impact on spindle tree shrubbery than cattle. Hence, in 2008, we laid out five transects in spindle tree shrubbery in the cattle area. In 2011, we laid out another five transects inside grazing exclusion areas, situated within the Kennemerduinen area, where grazing by the large grazers, but not deer species and rabbit, was excluded. One of the transects in these grazing exclusion areas was removed from

Table 1 Biomass density of each herbivore and total biomass density present in each area over time

Biomass density	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Kraansvlak										
E. bison	0	14.4	24.0	33.7	38.5	30.2	35.9	30.5	35.5	22.4
Konik horse	0	0	8.10	14.3	17.5	17.5	18.8	17.1	8.50	4.20
Rabbit	0.14	0.10	0.10	0.30	0.20	0.50	0.70	0.60	–	0.18
Roe deer	1.36	2.09	1.36	1.57	0.52	0.99	0.25	0.49	0.28	1.61
Fallow deer	2.37	2.37	3.16	2.37	3.95	4.35	2.28	8.08	9.84	1.16
Total	3.87	18.97	36.7	52.3	60.6	53.6	57.9	656.0	57.1	26.7
Kennemerduinen										
H. cattle	22.6	22.6	22.6	22.6	22.6	22.3	21.2	19.8	18.4	11.7
Konik horse	5.07	4.91	4.91	4.91	4.91	5.58	6.60	7.27	7.27	7.00
Shetland pony	5.41	5.07	4.74	4.57	4.57	4.23	4.23	4.23	3.72	3.50
Rabbit	0.07	0.15	0.12	0.15	0.07	0.12	0.14	0.03	–	–
Roe deer	1.75	2.38	1.72	1.77	0.83	1.32	0.43	0.58	0.47	0.58
Fallow deer	2.61	2.52	3.62	3.06	6.00	7.71	5.47	12.9	17.5	20.6
Total	37.5	37.7	37.7	37.71	39.0	41.3	38.1	44.8	47.3	43.4

–, no information available

The biomass density corresponds with the total amount of herbivore kilogram per hectare. The specific body weight of each herbivore species (average weight of adult males and females) was taken from diverse references (Armstrong 1996; Large Herbivore Network/ECNC 2009; Ministry of Agriculture, Food and Environment 2009) and correspond to 529 kg for European bison, 585 for Highland cattle, 350 kg for Konik horse and Shetland pony, 2 kg for rabbit, 23 kg for roe deer, and 58 kg for fallow deer. The biomass density of a species was calculated as the product of the number of individuals and individual weight of that species divided by the number of hectares of the respective grazing area. Rabbit counts took place on fixed transects, monitored by park rangers in spring and autumn every year. Each transect is visited eight times per season (Snater and Baeyens 1995). The average of the two highest numbers recorded in both seasons is taken as the minimum number population estimate for that year. The number of fallow deer and roe deer came also from annual counts by the park management authority according to the guidelines presented by the Vereniging Het Reewild (VHR) (Schoon 2014). During these counts, managers monitored fixed transects, three times per year for deer species and took the maximum number of these three counts as the minimum population estimate for that year. The number of E. bison, cattle, and horse reflects the actual total number of individuals as exactly known by the herd managers based on intense monitoring of the herds. Note that we assumed that the average biomass density of rabbit, fallow deer, and roe deer in the grazing exclusion areas was the same as the biomass density given for the cattle area (Kennemerduinen area) since these exclusion areas were located within this area and fences were easily passable by these species

the study because the fence was broken by a fallen tree and both cattle and horses were observed feeding inside the exclosure. In 2013, we added additional transects in maple tree (*Acer pseudoplatanus* L.) woodlands because we had started observing heavy use of this species, particularly debarking, by bison. We laid out three transects in the grazing exclusion area, three in the cattle area and one in the bison area. Only one maple tree woodland transect was laid out in the bison area because two of the original (2008) deciduous forest transects were dominated by *Acer pseudoplatanus* and could thus be used as maple tree woodland transects.

Vegetation measurements

We measured vegetation along the transects from February 2008 to May 2016 in the bison and cattle areas and from April 2013 to May 2016 in the grazing exclusion areas. Transects were measured at least once per year (in February or in August), with the exception of the year 2012 in which no transects were measured. The end and start of each transect were defined with a pole. At the start of measurements, we laid out a rope connecting these two poles as our transect line and recorded all woody plant individuals that were higher than 50 cm and of which the canopy crossed the transect line. We excluded individuals below 50 cm because it is easy to miss seedlings in tall grass, which could result in biases among habitats and transects. For each individual, we recorded the vitality, diameter, height, and type of use by herbivores for each of its stems according to different classes (Table 2). For each transect, we also monitored grass biomass using a disc pasture meter (a plastic disc with a diameter of 28.3 cm and a weight of 68 g), which was dropped along a centimeter scale (Bransby and Tainton 1977). The disc pasture meter was dropped every 2 m along the transect line (resulting in 25 measurements per transect) at 1 m to the right from the transect line. In addition, a tuft of grass from under the pasture disc was stretched along the scaled stick and the height of the third longest grass leaf was recorded. We measured the third longest

Table 2 Overview of measures and their units recorded for all woody species higher than 0.5 m on every permanent vegetation transect

Plant species	
Number of stems	
Viability of stems (3 nominal categories)	1. Stem is alive 2. Stem is dying 3. Stem is dead
Diameter (cm) at ankle or chest height	Ankle height: for shrubs Chest height: for trees and big shrubs
Type of use by herbivore (per stem) (4 nominal categories)	0. No use 1. Debarked 2. Branch eaten 3. Bud eaten

leaf because we wanted a proxy for the average height of the grass tuft, not the maximum height. The first or second longest leaf of a tuft is often outlying and not representative for this average height. Moreover, we estimated the percentage of aerial cover under the pasture disc for grass and forbs separately.

Data analysis

We recorded the vitality of all stems from each woody individual, and for the statistical analysis, we considered the vitality of the most viable stem as the vitality of the whole individual. We then calculated the proportion of living individuals per woody species per transect and tested if this proportion changed over time for each area separately (bison, cattle and grazing exclusion areas). Since assumptions of normality and homogeneity of variances were violated, we used non-parametric Spearman rank correlations. Similarly, we used Spearman rank correlations to test for trends over time in grass length, grass cover and herb cover. For this, we first converted the values of grass length (cm) into 12 ordinal classes (1 = 0–5 ≤ cm; 2 = 5–10 ≤ cm; etc.). In the analyses of grass and herb data, we only included data of the spindle tree transects of all grazing areas.

The extent to which the herbivores used different plants parts (bark, leaves, buds, branches) was recorded for every stem from each woody individual. To compare the use of different plant parts among areas and over time, we calculated a proportion for each type of use present for each woody individual that had been browsed by herbivores. We considered that an individual had one of the uses when at least one of its stems had a trace of that use. These proportions were arcsine transformed to meet assumptions of normality and homogeneity of variance. We performed two different types of analyses with these data. Firstly, for the 2016 data only, we compared the differences in the proportion of individuals of a woody species with different types of use among areas (European bison, cattle, and grazing exclusion areas) with a linear mixed-effect model. In these models, we used transect number nested within habitat type as random effect and woody species, grazing area, and their interaction as fixed effects. For these analyses, we only included transects located in the habitat types *Acer pseudoplatanus* and *Euonymus europaeus* because the three areas only had these two habitat types in common. We ran a model for all types of use combined and separate models for each type of use. Secondly, we compared the proportion of individuals with different types of use by herbivores between the first and the last year of measurements (2008 and 2016) for the European bison area only. Here, we used woody species, year of measurement, and their interaction as fixed effects and again transect number nested within habitat as random effect. We ran separate models for each type of use. For all analyses, we used the open source software R (R Core Team 2016).

Results

Trends in proportion of living individuals per species in the different grazing areas

The proportion of living *Euonymus europaeus* decreased significantly over the years in the bison ($r = -0.608$, $P < 0.001$), the cattle ($r = -0.675$, $P < 0.05$), and the grazing exclusion ($r = -0.840$, $P < 0.001$) areas (Fig. 2a). *Hippophae rhamnoides* ($r = -0.424$, $P < 0.001$) and *Sambucus nigra* L. ($r = -0.358$, $P < 0.05$) also decreased significantly in the bison area (Fig. 2b, c). Not enough individuals of these species were recorded on the permanent transects of cattle and grazing exclusion areas to test for trends. The proportion of *Ligustrum vulgare* L. ($r = -0.574$, $P < 0.05$) and *Crataegus monogyna* ($r = -0.648$, $P < 0.01$) decreased significantly in the grazing exclusion areas but not in the cattle and bison areas (Fig. 2d, e).

Different types of herbivore use in 2016 in the different grazing areas

Looking at all types of use combined, the proportion of *Acer pseudoplatanus* used by herbivores was significantly higher in the bison area than in the other areas, while *Crataegus monogyna* was used more in the cattle area than in the bison area. *Euonymus europaeus* was used more in the grazing exclusion area than in the bison area (Fig. 3a, Table 3). The proportion of individuals with browsed branches of *Crataegus monogyna* was higher in the cattle area than in the bison and grazing exclusion areas while *Ligustrum vulgare* had a higher proportion of individuals of which branches were eaten in the bison area than in the other areas. For *Acer pseudoplatanus*, the proportion of individuals with eaten branches was higher in the bison and the cattle areas

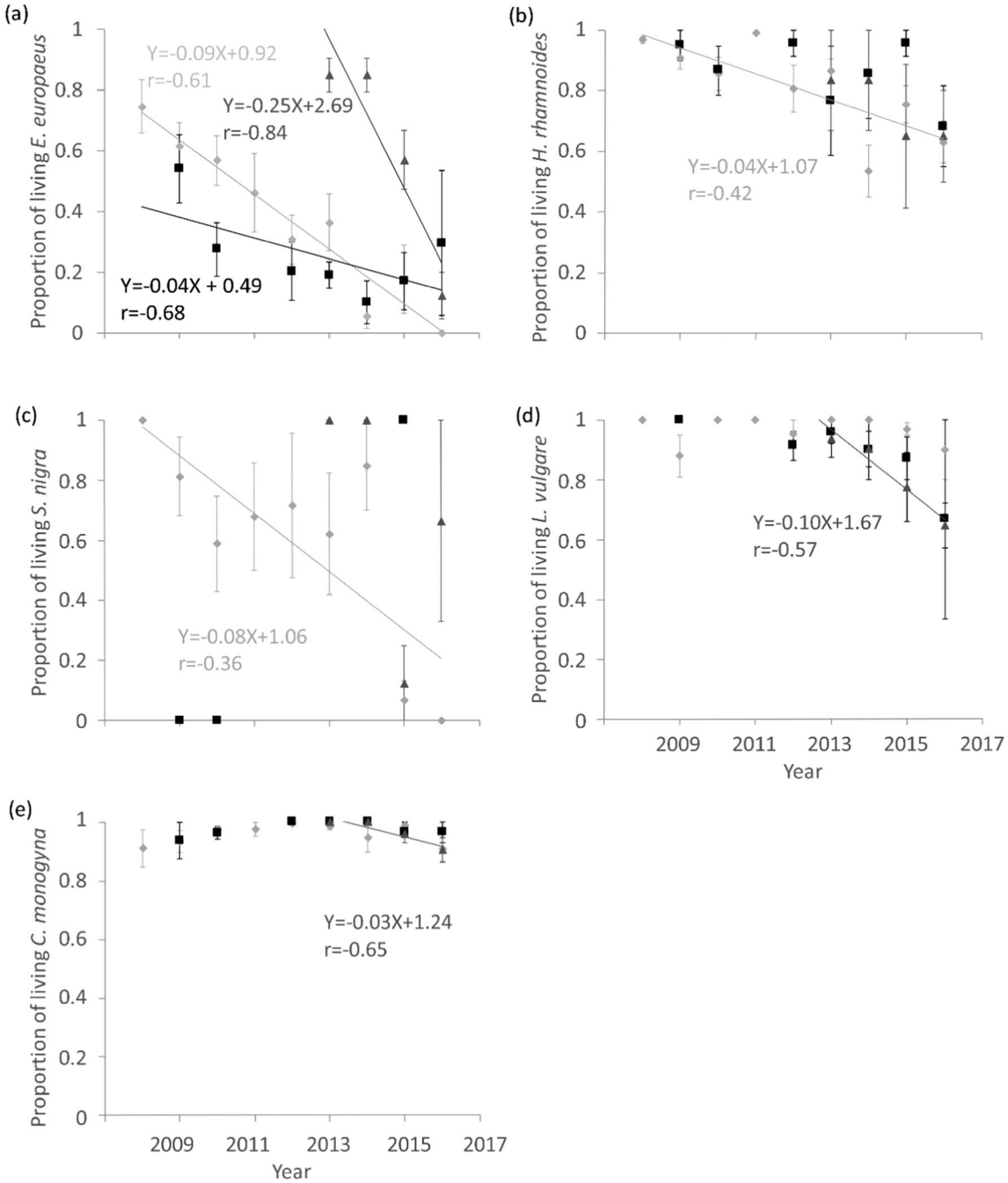

Fig. 2 Proportion of living *Euonymus europaeus* (**a**), *Hippophae rhamnoides* (**b**), *Sambucus nigra* (**c**), *Ligustrum vulgare* (**d**), and *Crataegus monogyna* (**e**) (mean ± SE) in the bison (light gray rhomboid symbols), the cattle (black squares symbols), and the grazing exclusion (dark gray triangular symbols) areas. Linear correlation lines were drawn based on significant levels ($P < 0.05$)

compared to the grazing exclosure. No branches were eaten from *Euonymus europaeus* in any of the three areas (Fig. 3b, Table 3). The proportion of debarked individuals of *Acer pseudoplatanus* was higher in the bison area than in the other areas. In contrast, *Euonymus europaeus* was debarked to a higher extent in grazing exclusion areas than in the other areas (Fig. 3c, Table 3). The proportion of individuals of *Ligustrum vulgare* with buds used was higher in grazing exclusion areas than in the other areas (Fig. 3d, Table 3). From the other woody species, no buds were eaten in any of the three areas (Fig. 3d, Table 3).

Difference in woody species use between start (2008) and end (2016) of study period in the bison area

In the bison area, *Sambucus nigra*, *Crataegus monogyna*, *Acer pseudoplatanus*, and *Ligustrum vulgare* were used more in 2016 than in 2008, while the proportion of individuals of

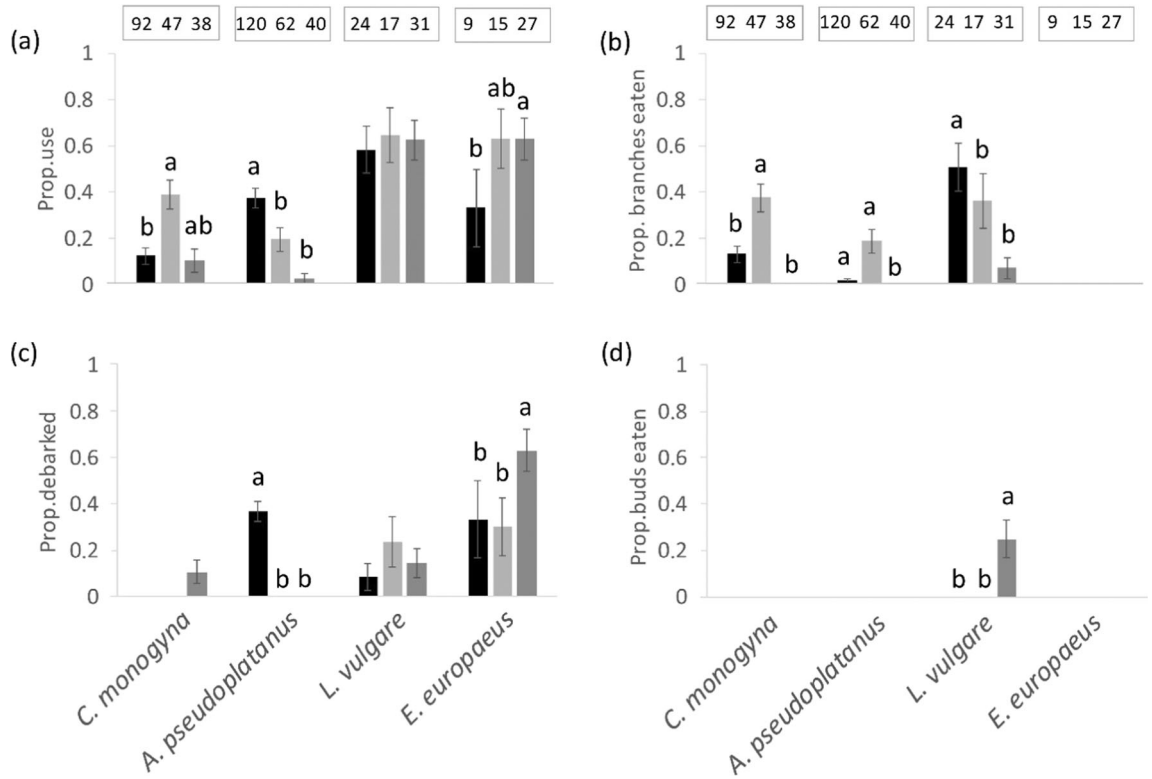

Fig. 3 Use of woody species in the bison (black bars), cattle (light gray bars), and grazing exclusion areas (dark gray bars) in 2016 (mean ± SE). **a** Proportion of woody species with any use. **b** Proportion of woody species with branches eaten. **c** Proportion of woody species debarked. **d** Proportion of woody species with buds eaten. Letters indicate significance among groups where groups with the same letter are not significantly different. Numbers above graphs indicate the number of woody species recorded in the transects of each area. Note that *H. rhamnoides* was not included in the figure because there were not enough individuals in the cattle and grazing exclusion areas

Euonymus europaeus used was lower in 2016 than in 2008 (Fig. 4a, Table 4). *Crataegus monogyna* and *Ligustrum vulgare* had a higher proportion of individuals with browsed branches in 2016 than in 2008 (Fig. 4b, Table 4), while higher proportions of *Sambucus nigra* and *Acer pseudoplatanus* were debarked in 2016 compared to 2008. In contrast, the proportion of *Euonymus europaeus* individuals that was debarked was significantly lower in 2016 than in 2008 (Fig. 4c, Table 4). Finally, the proportions of individuals of *Acer pseudoplatanus* and *Euonymus europaeus* with buds used were significantly lower in 2016 than in 2008 (Fig. 4d, Table 4). From the remaining species, no buds were eaten in any year (Fig. 4d, Table 4).

Changes in grass and herbaceous cover

Grass length and the proportion of grass cover declined over time in all the areas (Fig. 5b, Table 5), while there was a significant increase in the proportion of herb cover in the bison and cattle areas (Fig. 5c, Table 5).

Discussion

The impact of herbivores on woody vegetation was noticeable, and similar, in all three grazing regimes in the National Park Zuid-Kennemerland, particularly in terms of strong

Table 3 Results of a two-way ANOVA testing for an effect of woody species and grazing area, and their interaction, on different types of herbivore use in 2016

Source of variation	Woody species		Area		Woody species * area	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value
Prop. use	*14.22*	*< 0.001*	0.67	0.311	*8.85*	*< 0.001*
Prop. branches eaten	*10.66*	*< 0.001*	0.61	0.442	*10.83*	*< 0.001*
Prop. debarked	*22.46*	*< 0.001*	1.38	0.251	*8.35*	*< 0.001*
Prop. leaves eaten	2.56	0.054	0.06	0.802	1.73	0.161
Prop. buds eaten	*29.19*	*< 0.001*	1.79	0.192	*31.74*	*< 0.001*

Italic values refer to significant factors

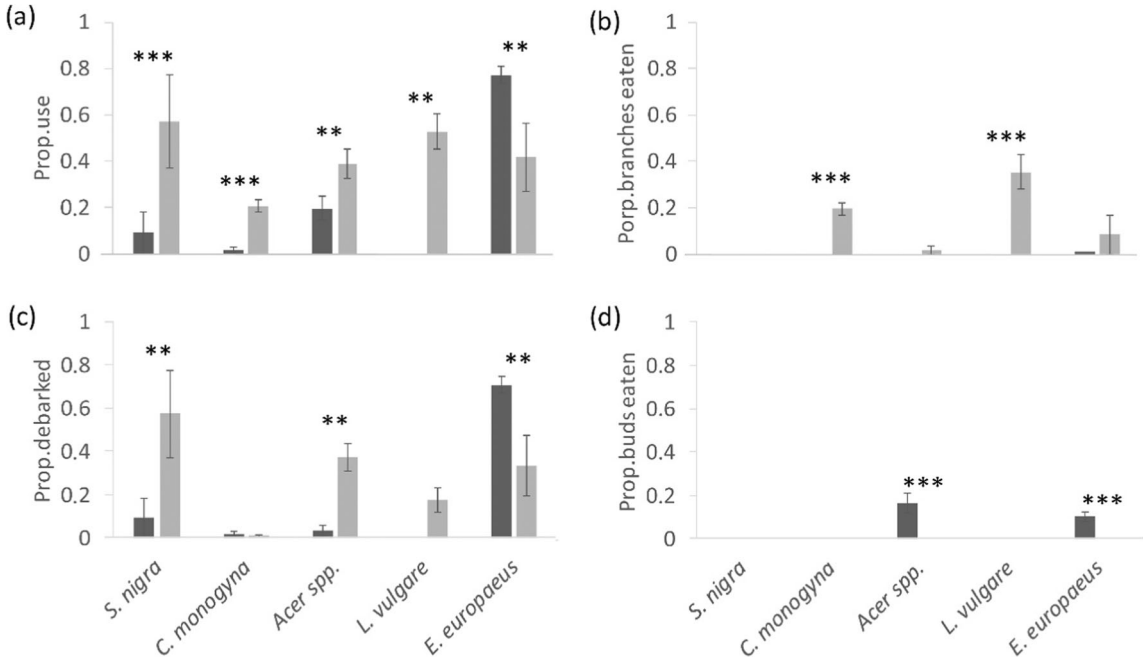

Fig. 4 Proportion of woody species used in the bison area in 2008 (dark gray bars) and 2016 (light gray bars) (mean ± SE). **a** Proportion of woody species with any use. **b** Proportion of woody species with branches eaten. **c** Proportion of woody species debarked. **d** Proportion of woody species with buds eaten. Asterisks indicate significant differences between rounds within woody species, with **($P < 0.01$) and ***($P < 0.001$). Note that *H. rhamnoides* was not included in the figure because there were not enough individuals in the cattle and grazing exclusion areas

declines in *Euonymus europaeus*. The extent to which the herbivores used the various woody species differed significantly among areas. Specifically, *Acer pseudoplatanus* was debarked in the bison area, whereas *Crataegus monogyna* twigs were browsed more in the cattle area. In grazing exclusion areas *Euonymus europaeus* bark and *Ligustrum vulgare* buds were eaten more than in bison and cattle areas. Changes in the grassland habitat were also similar across the three grazing areas, where grass length and the proportion of grass cover both declined over time, while the proportion of herb cover increased. These results confirm our first hypothesis that the vitality of certain woody species would decline over time, but we did not find evidence for a difference in the extent of this impact between E. bison and cattle grazing areas. In contrast, the patterns of herbivore impact were very similar among all three grazing areas, including the grazing exclusion areas.

Euonymus europaeus was the main species that declined strongly in all three grazing areas and the fact that the main herbivore use of this species was debarking suggests that this is the main cause of its decrease in vitality. The use of and preference for this species by European bison has been highlighted before (Borowski et al. 1967; Gębczyńska and Krasińska 1972; Terboganova 2014; Nevřelová and Ružičková 2015; Cromsigt et al. 2017). However, cattle (Kinnaird et al. 1979), horse (Kuiters et al. 2006), fallow deer (Gill 1992), and roe deer (Gill 1992) also debark woody species and may thus have been responsible for *Euonymus europaeus* debarking as well. Characteristics such as the softness and greenness of *E. europaeus* bark may be an important reason why ungulates highly prefer it for debarking (Kinnaird et al. 1979). The proportion of debarked *Euonymus europaeus* was higher in the grazing exclusion areas than in the bison and

Table 4 Results of a two-way ANOVA testing for an effect of woody species and measuring round (2008 or 2016), and their interaction, on different types of herbivore use in the bison area

Source of variation	Woody species		Round		Woody species * round	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value
Prop. use	*49.90*	*< 0.001*	*19.27*	*< 0.001*	*7.88*	*< 0.001*
Prop. branches eaten	*15.42*	*< 0.001*	*23.03*	*< 0.001*	*4.13*	*0.003*
Prop. debarked	*104.07*	*< 0.001*	*9.75*	*0.002*	*15.96*	*< 0.001*
Prop. leaves eaten	0.02	0.994	0.01	0.970	0.01	1
Prop. buds eaten	*3.33*	*0.010*	*15.25*	*0.001*	*6.65*	*< 0.001*

Italic values refer to significant factors

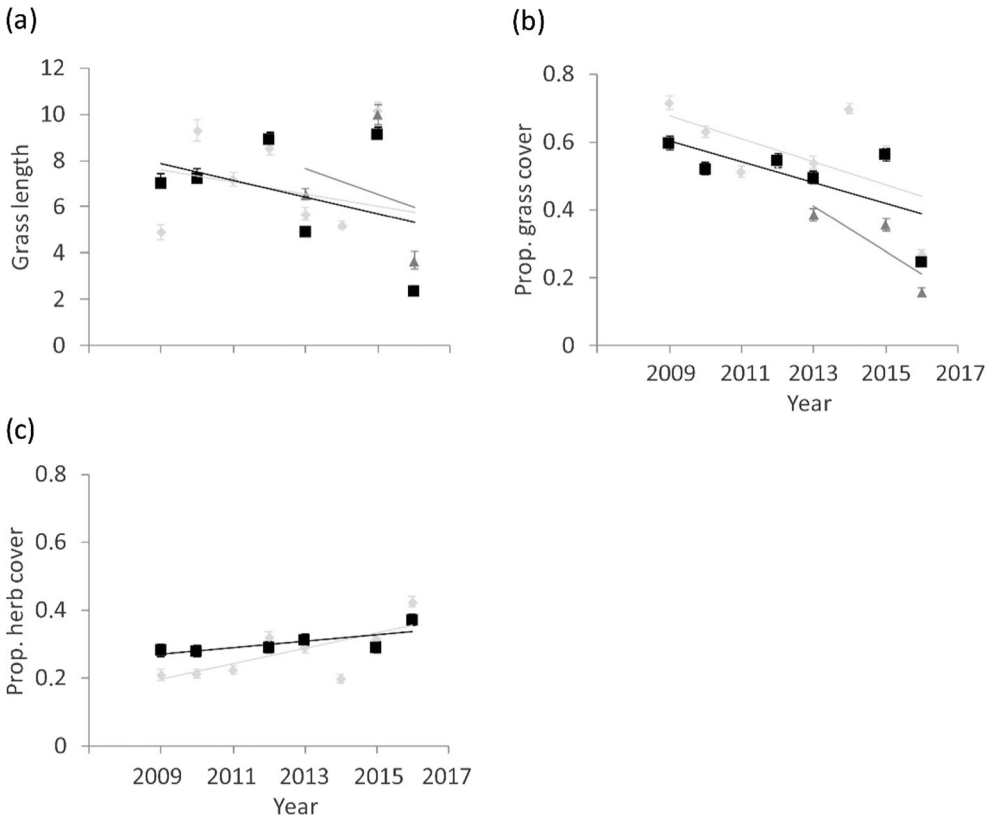

Fig. 5 **a** Variation in grass length, **b** proportion of grass cover, and **c** proportion of herb cover (mean ± SE) on the spindle tree transects over time in the bison (light gray rhomboid symbols), the cattle (black squares symbols), and the grazing exclusion (dark gray triangular symbols) areas. Linear correlation lines were drawn based on significant levels ($P < 0.05$)

the cattle area. The deer species, of which fallow deer was by far the most abundant, thus likely played an equally, if not more, important role in the declining vitality of this species than cattle, bison, and horse. Deer also debark in the middle of the summer (Storms et al. 2008; Saint-Andrieux et al. 2009) while debarking in summer is rare in the case of horses, cattle, and bison (Klich 2015; Cromsigt et al. 2017).

The decline in *Hippophae rhamnoides* in the bison area is perhaps surprising since this species has heavy structural defense through thorns. We recorded hardly any signs of feeding on this species. Most of the damage on *Hippophae rhamnoides* in fact consisted of broken branches and general trampling effects on shrubs (Cromsigt et al. 2017). Moreover, bison frequently walk through dense thorny *Hippophae rhamnoides* vegetation in contrast to the horses (*personal observations* by Esther Rodriguez and Cromsigt et al. 2017). The thick fur and skin of European bison in contrast to that of horses might explain this difference in behavior. Therefore, we conclude that the strong decline of *Hippophae rhamnoides* in the bison area is likely due to the physical impact of bison when these large herbivores move through the landscape to reach their preferred food sources, drinking places, or resting spots. Within the bison area, this has led to the opening up of dense shrubberies of this species. Unfortunately, we did not encounter enough *Hippophae rhamnoides* in the cattle and the grazing exclusion areas to test for similar effects there.

Table 5 Significance levels and correlation coefficients (rho) for Spearman correlations for the variation in grass length, the proportion of grass cover, and the proportion of herb cover over time for the spindle tree transects in the different grazing areas

	E. bison area	Cattle area	Grazing exclosure area
Grass length	−0.108**	−0.206*	−0.229*
Grass cover	−0.269**	−0.260*	−0.310*
Herb cover	0.236**	0.133*	n.s

Asterisks indicate significance levels, with *($0.05 < P < 0.01$) and **($P < 0.001$)

In the bison area, the herbivores switched their preferential use of tree species between the start and the end of the study period. The proportion of debarked *Euonymus europaeus* in the bison area was significantly lower in 2016 than in 2008. In 2008 we recorded 144 living *Euonymus europaeus* along our transects in contrast to only 9 in 2016. With this decreasing abundance of living *Euonymus europaeus* and increasing bison numbers in the bison area, herbivores switched to feed more on other woody species such as *Sambucus nigra*, *Acer pseudoplatanus*, *Ligustrum vulgare*, and *Crataegus monogyna*. The proportion of debarked *Sambucus nigra* and *Acer pseudoplatanus* and browsed *Crataegus monogyna* and *Ligustrum vulgare* was significantly higher in 2016 than in 2008. At the end of the study period, in 2016, *Acer pseudoplatanus* was used more in the bison area while *Crataegus monogyna* was used more in the cattle area. These

two species were not used in the grazing exclosures. The different use of *Acer pseudoplatanus* and *Crataegus monogyna* in bison and cattle area respectively reflected a different use of plant parts. The use of *Acer pseudoplatanus* in the bison area mostly consisted of bark use, while the use of *Crataegus monogyna* in the cattle area mostly reflected use of twigs. *Ligustrum vulgare* was used in all the areas but the type of use differed among areas. The proportion of *Ligustrum vulgare* with buds eaten was higher in the grazing exclosures than in the other areas, while the proportion of branches eaten was higher in the bison area than in the other areas. Cromsigt et al. (2017) found similar differences in use between grazing regimes by directly observing the feeding behavior of bison and cattle in our study areas. They also stressed that difference in use between bison and cattle area may at least partly be due to differences in the availability of tree species such as *A. pseudoplatanus* and *C. monogyna* between the grazing areas and not necessarily a difference between bison and cattle. Data from other Dutch grazing areas supports this, e.g., heavy debarking of *A. pseudoplatanus* in the Oostvaardersplassen area where grazers include cattle, horse, and red deer but not bison (Cornelissen 2017). Moreover, another explanation may lie in higher overall herbivore density in the bison area than in the cattle area.

The overall grazing activity in the bison and cattle areas and also similarly in the grazing exclosure areas led to a significant decrease in the grass length and the proportion of grass cover over time, while the proportion of herb cover increased significantly. This decrease in grass length and grass cover by herbivores is considered a key eco-engineering factor that provides opportunities for other plant species to establish and develop, increasing or maintaining the diversity of herbaceous species (Sternberg et al. 2000; Van Klink et al. 2016). It is particularly interesting to note that our results suggest that grazing regimes with bison may have similar effects on the grass layer as grazing regimes with cattle. Thus, there may be potential for also using European bison to increase variation in grass height and to reduce "grassification" in addition to their effects on woody plants. This is interesting because the European bison may have certain advantages over domestic cattle, e.g., in terms of their legal status as a wild species (see also the "Conclusion" section).

Conclusion

We presented the first results from a trophic rewilding initiative in the Netherlands where grazing by an herbivore community including European bison was compared with a grazing regime of an herbivore community including cattle and a grazing regime with neither cattle nor bison. As hypothesized, we found that all three grazing regimes led to a reduction in the vitality of woody plants, reduced grass height, and increased herb cover. However, these changes were largely similar for all grazing regimes. Surprisingly, the area with only fallow deer, roe deer, and rabbit grazing showed similar vegetation trends as the areas with bison or cattle. Moreover, variation in densities of the different herbivore species in the grazing areas did not allow for drawing strong conclusions about differences among herbivore species in terms of how they drive vegetation changes. For example, from 2009 onwards, the biomass of bison in Kraansvlak was almost twice higher than the biomass of cattle in Kennemerduinen. Moreover, between 2010 and 2014, Konik horse biomass was higher in Kraansvlak than in Kennemerduinen. As a result, for most of the study period, the total herbivore biomass density was clearly higher in Kraansvlak than in Kennemerduinen. However, we can still draw several important conclusions from our study. Firstly, a grazing regime where one replaces the role of cattle by European bison may lead to similar strong impacts on the vegetation, including impacts on grassland. This is relevant since European bison has a legal status as a wild large grazer in Europe while free-ranging cattle are domestic livestock with implications for management and ethical animal welfare issues. European bison can be an interesting addition, or alternative, to free-ranging cattle in ecological restoration initiatives. Secondly, we found similarly strong effects on the vegetation in the large grazer exclusion areas, where relatively high densities of fallow deer occurred. This suggests that intermediate-sized grazers, such as fallow deer, can play an equally important role in structuring vegetation communities than larger herbivores.

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