

## Research

### Fifty years of European ungulate dietary studies: a synthesis

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Over recent decades, ungulate populations across Europe have undergone a rapid recovery. While this constitutes a conservation success, there is increasing concern about their impacts on shared resources with humans. Understanding ungulate food choices is crucial for predicting such impacts. Numerous studies have focused on single species or communities at narrow spatial scales. Here, we used 265 published diets from 87 European studies to investigate patterns of resource use by four common deer species (moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and fallow deer *Dama dama*), and wild boar *Sus scrofa* at the continental scale. On average, deer diets separated mostly along a gradient from grass to browse. Fallow deer diets contained the most and moose diets the least amount of grass, but we also found large intraspecific variation among all deer species. Diets of roe deer, a presumed browser, frequently contained  $\geq 25\%$  grass. Wild boar diet contained grass in amounts similar to red deer but otherwise differed strongly from deer diets. All five ungulate species shifted to eating higher proportions of woody browse during winter. Habitat influenced variation in intraspecific diets, but the proportions of key forage types related to feeding type (i.e. grass for intermediate feeders red and fallow deer, and shrubs for the browsers moose and roe deer) remained fairly consistent across habitat types. In northern and central Europe, diet similarity between roe deer and red deer was highest during winter and spring and lowest during summer and autumn but remained constant across the seasons in southern Europe. We foresee that, as interspecific interactions driven by land-use and climatic changes increase across Europe, further monitoring and testing will be needed to understand the dynamics of dietary niche partitioning among ungulates.

Keywords: browser, dietary overlap, Europe, grazer, ungulate diets

#### Introduction

The past decades have witnessed a rapid recovery of ungulate populations across Europe (Deinet et al. 2013). Since the 1960s, ungulates have benefited from reduced exploitation and increased protection, coupled with changes in land-use such as the decline of

free-ranging livestock, land abandonment due to urbanization, the new agricultural practice of sowing winter-wheat, and the provision of supplementary feeding. Additionally, the widespread practice of clear-cutting in modern forestry has created abundant forage resulting from pioneer vegetation and replanting. Reintroduction programs and climate change with warmer, less snow-rich winters have also promoted an increase in ungulate numbers and expansions of species' ranges. The European moose *Alces alces* population, for example, increased by approximately 200% from 1960 to 2005, roe deer *Capreolus capreolus* by 250%, and that of red deer *Cervus elaphus* and wild boar *Sus scrofa* by 400% (Deinet et al. 2013).

As a result, areas once depauperate in ungulates are now home to unprecedented multispecies communities in landscapes that are heavily shaped by humans (Linnell et al. 2020). Under such novel conditions, balancing the ecosystem services provided by ungulates (e.g. meat provision, hunting opportunities, or rooting/forest pest reduction by wild boar) with adverse socio-economic impacts (e.g. damage to crops and forests (Bleier et al. 2012), and traffic collisions (Björnstig et al. 1986)), poses an enormous challenge (Linnell et al. 2020). While it has been well demonstrated that ungulates can exert a profound impact on the habitats and resources they utilize (McInnes et al. 1992, Frank et al. 2000, Palmer et al. 2004, Wolf et al. 2007), it is less understood what effect any changes to the size and composition of ungulate communities might have on such impacts.

Understanding food choices is crucial in addressing the impacts of ungulates on ecosystems and human resources, because satisfying dietary needs is one of the strongest drivers of ungulate behaviour. All ungulates experience energy-demanding cycles of reproduction coupled with periods of nutritional deprivation and climatic stress (Vavra and Riggs 2010). Their diets (i.e. the composition, quality and quantity of ingested foods), affects condition and survival from the level of individuals to that of populations. In this context, three aspects of trophic ecology are of particular importance: feeding type, diet flexibility and changes in interspecific dietary overlap. Knowledge of what drives feeding types and dietary changes is of key importance because it is linked to the impact of ungulate communities on vegetation, which in Europe often is a resource shared with humans (e.g. crops, forest plantations). Likewise, a more thorough understanding of dietary overlap is necessary to disentangle issues of resource sharing among ungulates, and how this may influence ungulate community composition and population dynamics. The latter can affect societal values (e.g. hunting opportunities or impacts on vegetation) because various ungulate species are likely to perceive the same habitats differently in terms of food choices. This may then lead to different degrees of utilization and ecosystem functions (Gordon 2003).

Ecologists have long been aware that different species of large herbivores favour different forages. Drawing initially on observations of complex African herbivore communities, ruminant herbivores were typically placed along a continuum

of feeding types from browsers to intermediate (or 'mixed') feeders and grazers (Van Zyl 1965, Jarman 1971, Hofmann and Stewart 1972). Browse (leaves and twigs of woody vegetation and non-woody dicots such as forbs) and grasses represent distinct food groups that differ in many characteristics (e.g. spatial distribution, biochemical and physico-mechanical properties) and create different challenges and constraints for animals feeding on them (Codron et al. 2019). Confusion over feeding types can arise if it is unclear whether classifications are meant to refer to the botanical composition of diets or the morphophysiological adaptations of ruminant species. It has been well established that relationships between morphophysiological traits and the efficacy of utilizing grass and browse exist (for comprehensive reviews see Clauss et al. 2008 and Codron et al. 2019) but such relationships should not be interpreted in the sense that a given adaptation is exclusively suitable for a specific diet (Clauss and Hofmann 2014). In this study, we follow Clauss et al. (2010) and refer to ruminant feeding types along the browser–intermediate feeder–grazer continuum in the context of botanical diet composition.

Another important driver of food resource partitioning among ruminants is body mass (Illius and Gordon 1992). Larger species are generally able to subsist on lower-quality forage due to larger intake rates relative to their metabolic rate (Müller et al. 2013).

An important reason for us to use the browser-to-grazer classification is that it clearly relates to the management issues highlighted above. The degree to which browse and grasses are utilized by wild herbivores is of particular interest since these food groups often represent shared resources with humans. In this sense, specialist browsers would play a different role in ungulate–forestry interactions than species that predominately graze, which may conflict more with the production of agricultural crops and livestock pasture. The continued emergence of novel multispecies ungulate communities across Europe raises the question, how different feeding types will interact over shared food resources and the direction multispecies systems are likely to shift as a consequence (Linnell et al. 2020). Although the body of literature on the dietary ecology of European ungulates is extensive, the multitude of analysis methods and classifications of diet components, and variations in temporal and spatial extent of the studies, have made direct comparisons and consolidation of the findings difficult. A number of excellent reviews have attempted this at the species level (e.g. roe deer, Tixier and Duncan 1996) and red deer (Gebert and Verheyden-Tixier 2001) or directed their focus to a specific area (e.g. Fennoscandia (Mysterud 2000)).

However, studies investigating ungulate diets for a range of species at the continental scale in Europe are currently missing. In this study, we therefore aim to assess the applicability of feeding types across large spatio-temporal gradients by using published diets of four ruminants (moose, roe deer, red deer and fallow deer *Dama dama*) and one hindgut fermenter (wild boar) to characterize species-level diet

composition. We chose these species because they occur widely throughout the continent and are driving most of the human–wildlife conflicts mentioned earlier. Moose and roe deer are commonly understood to be browsers, both in terms of their diet (Cederlund et al. 1980, Cornelis et al. 1999) and their ‘moose-type’ digestive physiology (Clauss et al. 2010). Red deer and fallow deer are viewed as intermediate feeders, i.e. able to switch between browse and grass dominated diets (Kerridge and Bullock 1991, Krojerova-Prokesova et al. 2010). Although the omnivorous wild boar does not fit within the classification of ruminant feeding types, we included it in our analyses because it is a key component of the current European ungulate community and utilizes many of the same plant food resources as ruminants (Genov 1981). In this study, we did not include body mass as an explanatory variable, since the body size range and the number of species in our analysis were very limited. As a result, we could not use species as replicates of different body size classes and species identity was thus heavily confounded with body mass. Our number of species was also too low to use body mass as covariate. To assess how the ‘browser/intermediate feeder/grazer’ classification applies at the continental scale, we tested the following hypotheses:

- Hypothesis 1. Ruminant diets should separate along a grass-to-browse gradient. Intermediate feeders (red deer and fallow deer) should show larger variation in diet along the browser-to-grazer continuum than browsers (moose and roe deer) and should display a seasonal change in diet towards woody browse in winter.
- Hypothesis 2. The diet of hindgut-fermenting, omnivorous wild boar should be distant from the ruminant deer even within the context of shared food categories, but the directionality of diet changes from the growing season to winter should be the same for all five ungulate species, i.e. towards woody browse. Consumption of animal matter by wild boar should be a major distinguishing factor from deer species.
- Hypothesis 3. Browsers should show less variable diet compositions across different habitat types than intermediate feeders as the latter are able to utilize a wider range of vegetation types, including grasses.
- Hypothesis 4. During the growing season, intraspecific diet similarity should be higher for browsers than for intermediate feeders because the latter can exploit both browse and grass (depending on local availability), whereas browsers would be restricted to the browsing niche. The increased variation in diet via utilization of grasses would mean a decrease in diet similarity. During winter, intraspecific diet similarity should be higher than during the growing season as the variety of available plants is reduced.
- Hypothesis 5. Interspecific diet similarity should be highest in winter when food availability is lowest and decrease during the growing season. The magnitude of seasonal changes in diet similarity should be linked to the severity of seasonality (i.e. be lowest in southern Europe).

## Material and methods

### Diet composition data set

We searched the Web of Science Core Collection for publications from 1965 to 2016 using the Boolean search terms: Topic: (moose OR ‘red deer’ OR ‘roe deer’ OR ‘fallow deer’ OR ‘wild boar’) AND (diet\* OR food\* OR forage\*). The searches were carried out on 27 November 2015 and 22 July 2016 and yielded a total of 2561 studies. These, we then manually filtered further for publications that focussed on Europe (with the exception of the Russian Federation) and contained complete quantitative diet compositions for ungulates, which were either free-ranging or, in one instance (Bruinderink et al. 1994), lived in large enclosures under near natural conditions. We excluded studies that quantified only part of the diet, for example summer browsing by moose on deciduous trees, and did not state these proportions in relation to the rest of the diet. Likewise, we did not include studies that contained only qualitative data such as a list of consumed plant species.

For diet compositions to be comparable, they must be expressed in the same unit, typically as percentages (Cornelis et al. 1999). Depending on the type of sample and analysis technique used, authors based the percentages of the food categories on various totals, including the dry weight of rumen content, volume of rumen content, number of faecal fragments, area of faecal fragments, frequency of occurrence, or a combination of these measurements. We standardized diet data over studies by assigning it to 11 food categories (Table 1), which best reflected the categories used among authors. When categories were reported at a relatively coarse resolution (for example, Marinucci et al. (2005) pooled deciduous trees and shrubs), we divided the reported value evenly over the respective categories (Marchand et al. 2013). Conversely, we aggregated diet data when it was presented at finer taxonomic resolutions (e.g. at plant species level). In cases of repeated measurements for the same location, for example over several consecutive summers, we averaged the reported values and did the same for the few instances ( $n=4$  publications) when diet was presented separately for males and females. ‘Browse’ in this study encompasses leaves and twigs from woody vegetation (shrubs, deciduous trees and conifers) and forbs. ‘Woody browse’ refers to leaves and twigs (which were frequently not distinguished in the literature) from woody vegetation only.

As time units, we chose the annual seasons because they represented the most commonly used temporal resolution. When given, we kept the authors’ classification assuming that ‘spring’ generally refers to the beginning of the growing season, ‘summer’ represents the peak of biomass availability, ‘autumn’ marks the period of vegetation senescence, and ‘winter’ is characterized by snowfall and/or vegetation dormancy (Bison et al. 2015). When monthly data was reported, we used the meteorological seasons for the northern hemisphere (Deutscher Wetterdienst – <[www.dwd.de/DE/](http://www.dwd.de/DE/)

Table 1. Food categories used for the standardization of reported diets. 'Shrubs', 'Deciduous trees' and 'Coniferous trees' encompass both leaves and twigs as they were frequently not distinguished in the literature.

Category	Description
Grasses	Graminoids (Poaceae, Cyperaceae and Juncaceae)
Forbs	Herbaceous flowering plants that are not a graminoid
FLH	Ferns, lycopods and horsetails
Shrubs	Shrubs and woody climbers (e.g. <i>Clematis</i> spp., <i>Lonicera</i> spp.)
Deciduous trees	Deciduous trees and Ivy ( <i>Hedera helix</i> )
Coniferous trees	Coniferous trees
Fruits and seeds	Fruits and seeds unless reported as agricultural crops
Fungi	Fungi
Crops	All agricultural plants if categorized as such by the author or if identifiable within food categories, e.g. wheat ( <i>Triticum</i> spp.) as a fraction of 'grasses'
Non-plant food	Vertebrates and invertebrates
Other	Unidentified fragments, lichens, mosses and algae

service/lexikon/ Functions/glossar.html?lv2=101304&lv3=101324>.) and calculated averages accordingly.

In cases where the sum of food proportions slightly deviated from 100 percent (due to rounding at the category level), we standardized to 100 percent. For every study site, we also

recorded the geographic coordinates in decimal degrees and the habitat type. To address large-scale biogeographical differences, we divided Europe into a northern, central and southern region based on the first and third quartiles of the latitudinal extent of the study sites (Fig. 1).

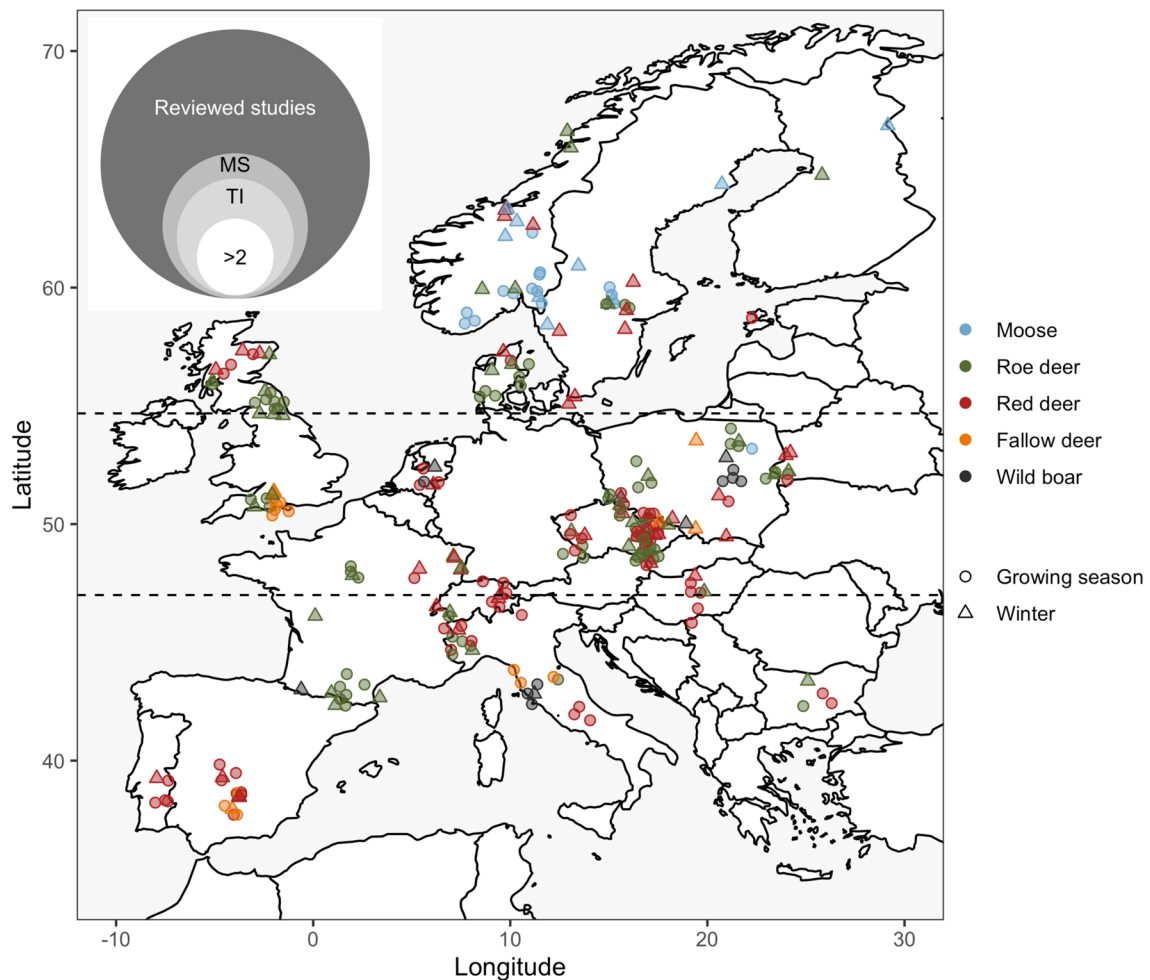


Figure 1. Map showing the locations of 265 diet compositions. The colours represent species while shapes denote the season. Dashed lines demarcate the boundaries between northern, central and southern Europe. The inset figure shows the proportions of multispecies diet studies (MS), the subset of those which focussed on trophic interactions (TI), and included more than two species (> 2).



## Hypothesis testing

### Hypotheses 1 and 2

To illustrate the range and distribution of browse and grass consumption by the five ungulate species, we plotted the proportions extracted from the literature and fitted density isopleths to the diet data points for each species (Fig. 2). To investigate the separation of the deer species and wild boar in terms of their use of grasses, woody browse and other food items, we used equilateral mixture triangles (EMT; Raubenheimer 2011). A species' nutritional geometry as well as the direction and magnitude of seasonal changes in diet can then be illustrated by vectors within the EMT (Fig. 3). The seasonal change was quantified as the magnitude of the vectors, i.e. their length between the coordinates of growing season and winter diets in 3-dimensional space. It was calculated as an Euclidian distance using R function *dist()*. To visualize patterns in diet dissimilarity within and among species, we calculated the Bray–Curtis dissimilarity between each pair of diets and ordinated these values using non-metric multidimensional scaling (NMDS) (Kartzinel et al. 2015, Pansu et al. 2019) as provided in R package *vegan* (Oksanen et al. 2017).

### Hypothesis 3

For each ungulate species, we determined the diet composition during the growing season and winter in each habitat type. We then used G-tests of independence (MacDonald 2014), followed by pairwise comparisons and Holm

corrections of the p-values, to test whether ungulate diet compositions within species differed between habitat types.

### Hypotheses 4 and 5

We used R package *spaa* (Zhang 2016) to calculate Pianka's index as a commonly used measure for dietary niche overlap (1 = complete overlap, 0 = total separation) (Putman 1996, Azorit et al. 2012, Lovari et al. 2014). Because 'overlap' implies the use of resources by organisms occurring at the same location at the same time, which was not the case for our data, we adopted the term 'diet similarity' instead. Thus, higher values of Pianka's index indicate increasing similarity in diet composition (1 = identical diets). Intraspecific diet similarity was calculated for all five ungulate species for the growing season and winter. To investigate diet similarity between different feeding types (i.e. interspecific similarity), we focused primarily on roe deer (a browser) and red deer (an intermediate feeder) because they were the only species for which diet data for the three European regions and all seasons were available. Following Mysterud (2000), we also calculated Pearson's correlation ( $r_p$ ) between diet similarity (Pianka's index; log-transformed) in the growing season and winter and differences in our feeding types. We quantified differences between species of the same feeding type as 0.5 (i.e. for the browser pair moose – roe deer and the intermediate feeder pair red deer – fallow deer). We quantified the difference between browsers and red deer as 1 (moose and roe deer – red deer), since red deer is suggested to be closer to strict browsers than to strict grazers (Hofmann 1989), and between browsers and fallow deer as 1.5 (moose

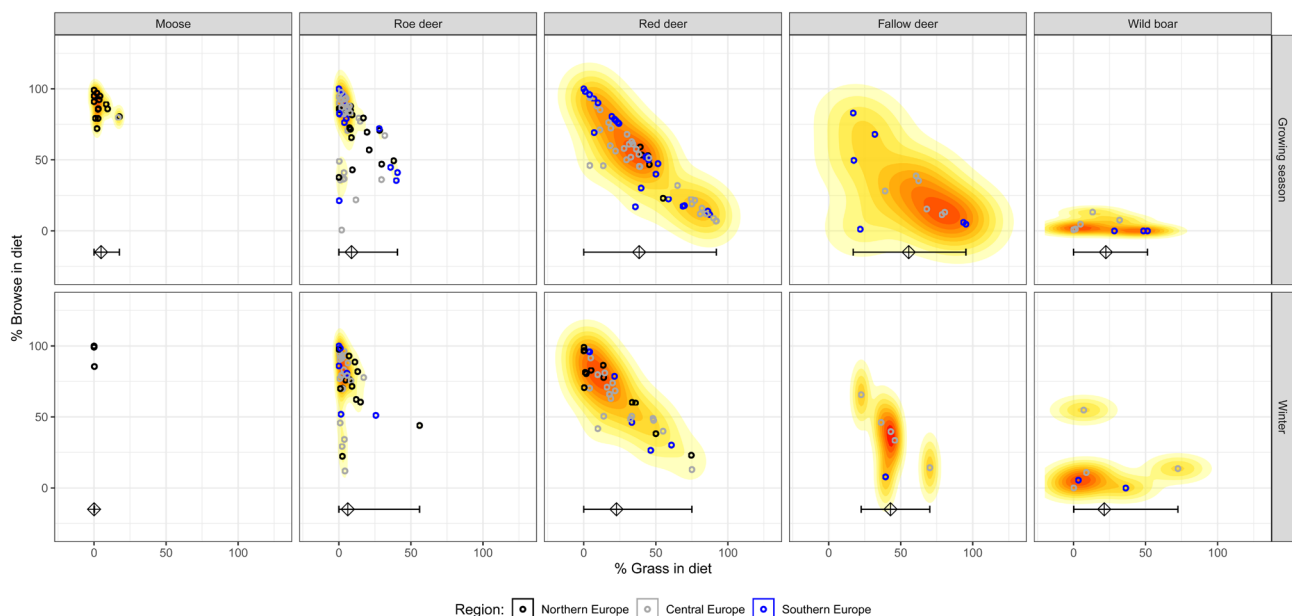


Figure 2. Utilization of grass and browse (shrubs, deciduous trees, conifers and forbs) by five ungulate species during the growing season and winter. Each circle represents a diet profile extracted from the literature. Circle colours indicate the study location within the three European regions. Density isopleths highlight the data distribution, with shading towards darker tones (red) corresponding to higher density, i.e. the most characteristic fraction of the data. Black diamonds indicate the mean proportion of grass in the diets and error bars extend to minimum and maximum values. Note that some food items (e.g. fruits and seeds or non-plant food) are not included and the values for x and y consequently do not sum up to 100%.

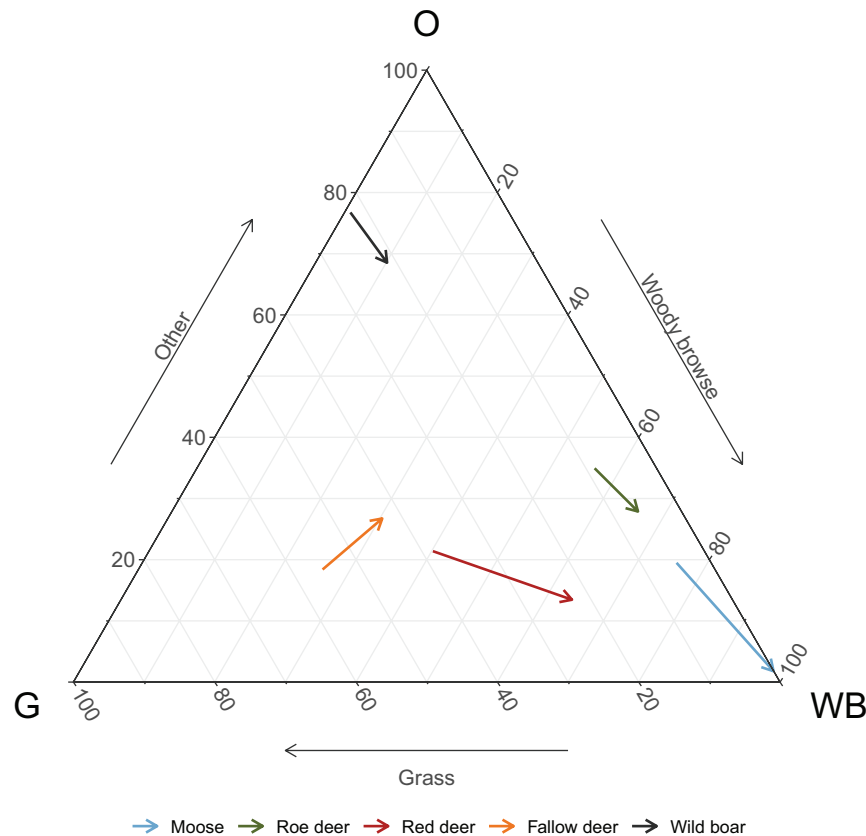


Figure 3. Equilateral mixture triangle showing the separation of diets within the dimensions of grasses (G), woody browse (WB) and other food items (O). The arrows indicate the changes in average diet composition from the growing season (blunt ends) to winter (arrow heads) with colours denoting the different ungulate species.

and roe deer – fallow deer) since fallow deer is one of the most grazer-like cervids (Putman et al. 1993). Finally, we assessed the difference between ruminants and non-ruminants as 3 (cervids – wild boar).

All analyses were carried out using R (<www.r-project.org>) with a significance level of  $\alpha = 0.05$  for statistical tests.

## Results

In total, 87 studies (Supplementary material Appendix 1 Table A1) passed our filtering criteria, i.e. focussed on Europe and reported complete diets for at least one season for one of the five ungulate species in this study. This corresponded to 265 diet compositions as several studies included multiple species, seasons and locations. Observations spanned 17 countries from 66° to 38°N and 10°W to 28°E. The majority of studies (71%) focussed on a single species and only 8% investigated trophic interactions between more than two species. Summary statistics for the diet composition of each ungulate species and season are provided in Supplementary material Appendix 1 Table A1.

### Hypotheses 1 and 2

As expected for intermediate feeders, the diets of red and fallow deer spanned the whole gradient from grass to browse

compositions during the growing season (Fig. 2). On average, fallow deer consumed higher proportions of grass (56%) than red deer (38%). During winter, the diets of red and fallow deer became more similar to moose and roe deer due to a decrease of grasses in their diets (fallow deer: –13%, red deer: –15%; Fig. 2). Moose and roe deer diets were dominated by browse during both the growing season and winter. Moose consumed virtually no grass in winter (< 1 %) and only very little (5%) during the growing season. Roe deer utilized grasses to a greater degree than moose (9% during the growing season and 6% in winter) but on average less than red or fallow deer. With one exception, the proportion of grass in roe deer diets never exceeded 50% but diets containing > 25% grass were not uncommon during the growing season. Grass consumption by wild boar was in between roe deer and red deer (~ 20% during the growing season and winter) but utilization of browse was generally much lower than for any of the cervids. The variation in the proportions of grass and browse in the diets of any of the five ungulate species appeared to be unrelated to the three European regions (Fig. 2) and likely reflects finer-scale variation in local food availability instead.

In the context of an equilateral mixture triangle (Fig. 3), the cervid species' diets separated mostly along the gradient from grasses to woody browse in the order of fallow deer > red deer > roe deer > moose. Wild boar diet was markedly

different from the cervids, owing to larger proportions of food items other than browse and grass (e.g. fruits, seeds and non-plant food). All five ungulate species displayed a change in diet from the growing season to winter, generally towards an increase in woody browse. The seasonal change was highest for red deer (29.5 units) and lowest for roe deer (12.2 units). NMDS ordination showed substantial similarities of feeding niches among cervid species (Supplementary material Appendix 1 Fig. A1). The feeding niche of moose was nested within that of roe deer during the growing season and was least similar to fallow deer. Niche space was smallest for moose (indicating little dissimilarity between reported diets) and largest for roe deer. The non-overlapping parts of the niche space polygons between browsers and intermediate feeders were associated with grass. The feeding niche of wild boar separated from the cervids during the growing season and only minimally overlapped in winter.

### Hypothesis 3

Global G-tests for independence were significant ( $p < 0.05$ ) for all species in both winter and the growing season, indicating different diet compositions in different habitats (Fig. 4). Pairwise post hoc comparisons showed significant differences in intraspecific diet similarity between most habitat types. Despite these differences, major food items linked to feeding type, e.g. grasses (intermediate feeders) or forbs and shrubs (browsers), showed similar intraspecific proportions across habitats.

### Hypotheses 4 and 5

Intraspecific diet similarity was highest for moose, followed by fallow deer in the growing season and vice versa during winter. The omnivorous, hindgut-fermenting wild boar

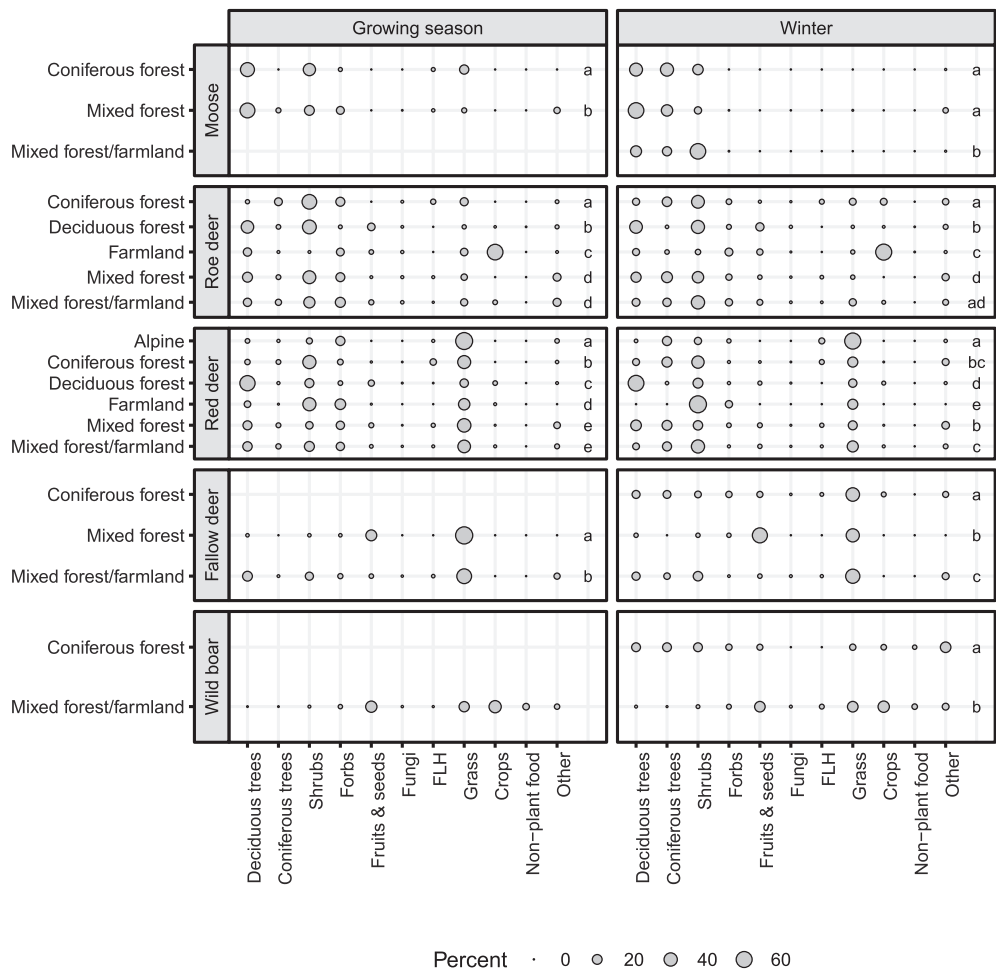


Figure 4. Average diet composition by habitat type and season for five ungulate species. The growing season corresponds to spring, summer and autumn. Within each species and season, habitat specific diet compositions connected by the same letter do not significantly differ ( $p \geq 0.05$ ), based on pairwise G-tests for independence with Holm-corrected p-values. For example, the diet composition of red deer in 'Coniferous forests' during winter is not significantly different from those of in 'Mixed forest' and 'Mixed forest/farmland' but different from diets in 'Alpine', 'Deciduous forest' and 'Farmland' habitats. Diet proportions across rows add up to 100%.

Table 2. Means and 95% confidence intervals of intraspecific diet similarity (Pianka's index) for five ungulate species during the growing season (spring to autumn) and winter. Mean values are presented in descending order within seasons.

Season	Species	Mean diet similarity (95% CI)
Growing season	moose	0.76 (0.72–0.80)
	fallow deer	0.68 (0.61–0.75)
	red deer	0.58 (0.57–0.60)
	roe deer	0.53 (0.52–0.54)
	wild boar	0.49 (0.34–0.63)
Winter	fallow deer	0.74 (0.65–0.83)
	moose	0.70 (0.63–0.77)
	red deer	0.56 (0.54–0.57)
	roe deer	0.53 (0.51–0.55)
	wild boar	0.30 (0.14–0.46)

showed the lowest intraspecific diet similarity. Seasonal differences in intraspecific diet similarity were generally small (Table 2).

Interspecific diet similarity between roe and red deer was highest in spring. In northern and central Europe, diet similarity declined during summer and autumn and strongly increased again during winter, creating a distinct U-shaped pattern, which was most pronounced in northern Europe (Fig. 5). In southern Europe, interspecific diet similarity remained relatively constant across seasons. There was a negative correlation between difference in feeding type and diet similarity during the growing season ( $r_p = -0.45$ ,  $p < 0.001$ ) and winter ( $r_p = -0.46$ ,  $p < 0.001$ ), i.e. the greater the difference between species (e.g. ruminant deer and non-ruminant wild boar) the less similar their diets.

## Discussion

From the literature spanning the past five decades, we assembled a thorough account of diet compositions for five key European ungulate species on a continental scale. These data allowed us to investigate several hypotheses arising from general ungulate trophic ecology, particularly with regard to the utilization of the main forage types (grass and browse). Our study also highlights several limitations of the currently available data. In the following, we will first discuss our results in the context of our five initial hypotheses, address their applicability to the current situation in Europe and conclude with a series of recommendations for future research.

### Hypothesis 1

Consistent with our expectations, separation between the four deer species occurred mostly along a gradient from grasses to woody browse in their diet (Fig. 3). Red and fallow deer as intermediate feeders showed a large variation in the proportion of grasses in their diets during the growing season and changed to a more browser-like diet, with high proportions of woody browse and less grass, in winter. This is likely a response to reduced availability of grasses and forbs during

winter. Moose did consume some grass in our data set, but it was rare (Fig. 2). This result supports the view that ruminants with a 'moose-type' digestion have a low threshold in % grass intake above which their digestion is less efficient, due to the morphophysiological adaptations of the digestive tract (Codron et al. 2019). Similar to moose, roe deer diets were generally dominated by browse but, notably, grass-rich diets were also common (Fig. 2). In spring, the average proportion of grass in roe deer diet was twice as high as during the other seasons (~14% versus ~7%, respectively; Supplementary material Appendix 1 Table A1). The higher utilization of grasses during spring might be explained by the abundance of young grasses during this season, which are easier to digest than their mature, more lignified versions later in the year (Lozano 2015).

### Hypothesis 2

Wild boar diet was notably different from the cervids. Although wild boar frequently consumed grasses in proportions similar to those of red deer, their diets contained very little browse and instead higher amounts of fruits, seeds and crops. However, proportions of browse in their diet increased during the winter, which was consistent with results for the cervids. The reported proportions of non-plant foods in wild boar diets were typically less than 10%, and thus a less important differentiator than we expected (Supplementary material Appendix 1 Table A1). Small amounts (< 0.2%) of ingested invertebrates were also reported for roe deer by Holisova et al. (1986) and Cransac et al. (2001).

### Hypothesis 3

We found that habitat type significantly influenced intra-specific variation in diets for all species. We, therefore, did not find support for our hypothesis that habitat types would influence the diets of browsers (moose and roe deer) less than diets of intermediate feeders (red and fallow deer). However, analyses were hampered by the fact that habitat descriptions in the studies were often quite general. Moreover, we also did not have diet data for all species in all habitat types. It is nevertheless noticeable that proportions of the key forage types, such as grasses for intermediate feeders or shrubs for browsers, were consistent across habitats. Unfortunately, measurements of food availability were missing from many studies and we were therefore unable to investigate food preferences and selectivity. But using habitat types as a proxy for food availability allowed for some useful insights. For example, consumption of conifer browse by all ungulates was low during the growing season and increased in winter (Fig. 4, Supplementary material Appendix 1 Table A1). This suggests that conifers may be an important food source during winter because the availability of other, more preferred food items is very low (Månsson et al. 2007). In fact, the availability of highly preferred plants, rather than the low availability of conifers, likely explains the low proportion of coniferous browse consumed by roe and red deer during winter in



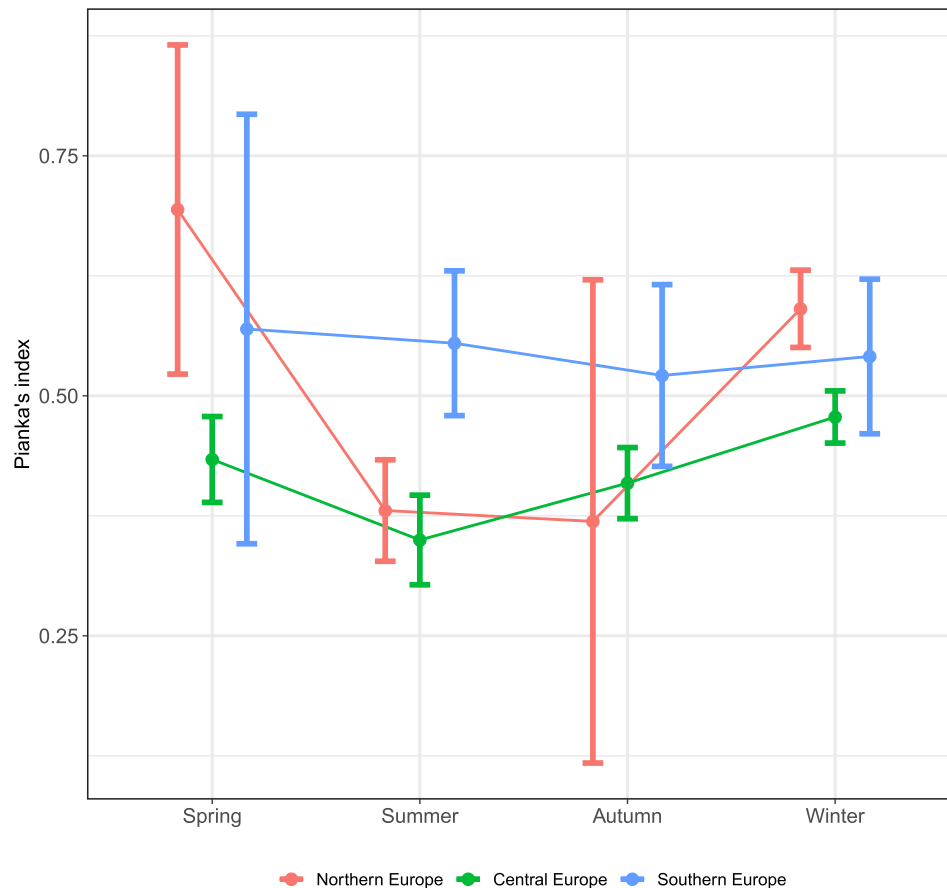


Figure 5. Mean interspecific diet similarity (Pianka's index) between roe deer and red deer across seasons and in the three different European regions. The error bars denote 95% confidence intervals. Seasonal differences in diet are most pronounced (larger changes in Pianka's index) in northern Europe and smallest in southern Europe.

farmlands and deciduous forests. Similarly, the ready availability of broadleaf trees in deciduous forests probably explains why their proportion in red deer diets is higher there than in other habitat types. The flexibility of diet use by roe deer, once thought of as a forest species (and representative of a 'moose-type' ruminant; Clauss et al. 2010), is particularly noteworthy and confirms previous studies indicating that roe deer are quite plastic in response to a reduction in woodland cover both behaviourally (Hewison et al. 2001) and in terms of their digestive system (Serrano Ferron et al. 2012). Wild boar also commonly frequent agricultural areas, particularly when crops are ripening (Herrero et al. 2006, Keuling et al. 2009, Thurfjell et al. 2009). Our review confirmed this relatively high use of agricultural crop plants, in farmland habitats, by roe deer and wild boar. Our data do not reflect all habitat types in which the five ungulates species occur because they are limited to studies that reported complete diets. These may be biased towards habitats in which a given species of interest is most common such as wild boar in agricultural areas in the context of crop damage. It is, however, indicative of the flexibility of intermediate feeders that red deer diets were reported for the widest range of habitats including alpine areas above the treeline, where red deer subsisted mostly on grasses on shrubs.

#### Hypothesis 4

Based on our broad food categories we expected that browser (moose and roe deer) diets would be confined largely to browse and thus show higher intraspecific diet similarity than the intermediate feeders (red deer and fallow deer), which also utilize grasses. This expectation was only partially supported by our results. While moose did show the highest intraspecific diet similarity (Table 2), values for fallow deer were almost equally high. Intraspecific diet similarity for roe deer was slightly lower than for red deer, mostly due to the medium amounts of grasses in roe deer diet. Moose and fallow deer showed the highest intraspecific diet similarity values because only a few of the food categories dominated their diets; woody browse (deciduous trees, conifers and shrubs) for moose and grasses for fallow deer. Roe deer, on the contrary, utilized all the food categories even more variably than red deer and thus had the lowest intraspecific values for Pianka's index (diet similarity) of all cervids but still higher than for the omnivorous wild boar. These findings highlight the difficulty with standardizing diet data from multiple sources and different taxonomic resolutions. The necessary pooling of plant species into main food categories will inevitably obscure fine-scale differences in resource use among species (Abrams 1980). For example,

Mysterud (2000) found that for ungulates in Fennoscandia, diet overlap was 12–31% higher when calculated from main plant groups than when calculated based on individual plant species. This probably also explains why we found only small differences in mean intraspecific diet similarity between winter and the growing season.

## Hypothesis 5

As expected, we found that the magnitude of seasonal changes in interspecific diet similarity between roe deer and red deer declined from northern to southern Europe. In northern and central Europe, the annual pattern of diet similarity showed a distinct U-shape with similarity being lowest during summer and autumn (Fig. 5). These results corroborate the findings by other authors in northern and central Europe. For example Putman (1996), who also used Pianka's index as a measure of dietary overlap, found a decline from 0.47 (winter) to 0.39 (summer) for red and roe deer in the New Forest area of England, and (Petrak 1993) reported a decline from 0.75 (mid-April) to 0.22 (mid-July) for the Eifel area (western Germany/Belgium) using an overlap index suggested by Colwell and Futuyma (1971). While diet similarity was high during the winter, as we had predicted, it did not differ much from the values in spring. In northern Europe, diet similarity during spring was even higher than in winter albeit with wide, overlapping confidence intervals. A possible explanation for high similarity in spring is that both species utilize the same fresh vegetation emerging during that period, thereby increasing diet similarity (Schoener 1974). The lower values for diet similarity in northern and central Europe during the summer and autumn, when food availability is at its highest and most diverse, probably resulted from the species switching to their preferred diets according to feeding type, with roe deer prioritizing browse and red deer increasing intake of grasses. Consistent with our expectations, interspecific diet similarity remained fairly constant throughout the year in southern Europe where a milder climate may mitigate seasonal changes in the variety and abundance of plants (i.e. food availability) and winter places less of a constraint on food supply than in northern Europe (Minder 2012). The low seasonal variation in diet similarity we found for roe deer and red deer in southern Europe reflects the findings of other authors. For example, Azorit et al. (2012) reported a diet overlap between sympatric red deer and fallow deer in Spain of approximately 0.6 (Pianka's index) across the year (with a peak of 0.79 in May–June) and Lovari et al. (2014) found a continuously high diet overlap between red deer and Apennine chamois *Rupicapra pyrenaica ornata* from spring to autumn in central Italy. This suggests, that in areas with low seasonality, variation in diet similarity within and between large herbivores species may be driven more by spatial rather than seasonal differences in food availability.

Without information about the availability of utilized food resources it is difficult to infer the potential for competition from measures of diet similarity alone. Unfortunately, many

of the studies in our review did not report food availability so we could not investigate competitive interactions among the ungulates. This stresses that we need studies that simultaneously investigate diet use and the quantity and quality of available forage in multispecies ungulate communities. Changes towards less nutritious diets in one competitor in the presence of others could then be an early indication of competition (Suryawanshi et al. 2010, Landman et al. 2013). What the diet data from across Europe does illustrate, however, is the importance of trees and shrubs as a food source for all four deer species throughout the year and particularly during winter. In today's Europe, the availability of these key food items, especially those that correspond to commercial timber species, depends almost entirely on forest management practices. As these tree species form a shared resource between humans and ungulates, it might be advisable to evaluate limits in their availability to ungulates not only in terms of natural constraints (e.g. site productivity, growth rate, tolerance to damage and regenerative capacity) but also from the angle of wildlife acceptance capacity (Decker and Purdy 1988), i.e. the level of ungulate damage that is acceptable before ungulates are either reduced in number through hunting or their access to forage artificially restricted through measures such as fencing.

Moose appeared to be the most restricted in their diet diversity and was the strictest browser, with only very low amounts of grass in their diets (typically < 10%). This may make moose populations sensitive to the influx of large numbers of intermediate feeders, red and fallow deer, into areas previously dominated by browsers, moose and roe deer. The added browsing pressure of the intermediate feeders could lead to a decline in both the quality and quantity of woody vegetation as has been shown for the shrub layer in boreal forests (Melis et al. 2006, Speed et al. 2014). While the intermediate feeders would be able to compensate to some extent for the reduced availability of browse by switching to grass, stricter browsers like moose might be unable to. Such a scenario is currently developing in northern Sweden, where red and fallow deer are extending their ranges into territories previously dominated by moose (Bergström and Danell 2009, Deinet et al. 2013). Although moose seem to be poorly adapted to digest grasses (Clauss et al. 2010) it may nevertheless be possible for them to feed on higher proportions of grass than their observed average diet currently suggests, e.g. during periods of food shortage (Schwartz and Hundertmark 1993) in captivity (Lechner et al. 2010), or when supplementary fed with grass silage (Felton et al. 2020). These examples highlight the challenges but also the unique opportunities offered by the Europe-wide emergence of novel ungulate assemblies (Linnell et al. 2020).

One of the most important take-home messages of our review is that it indicated an enormous bias towards studies that looked at diet use of single (62 out of the 87 studies) or at most two ungulate species (79 of the studies) simultaneously. Extremely few have thus explored trophic interactions among multiple sympatric ungulate species and the spatial

and temporal partitioning of food among these species relative to available food. We thus encourage future research of ungulate trophic ecology to place more emphasis on multispecies systems and on using a standardized method to assess diets. Technological advances, like the rapid emergence of DNA metabarcoding (Taberlet et al. 2018), will hugely support these efforts by enabling the processing of large amounts of samples from multiple species in much shorter time and at a lower cost than what has previously been feasible with classical methods like micro- and macrohistology. Molecular methods can provide higher taxonomic resolution of diets (Nichols et al. 2016), facilitate investigation of fine-scale resource partitioning and expand our understanding of diet plasticity (Kowalczyk et al. 2019). DNA analysis also makes it possible to investigate the links between diet and the gut microbiome of ruminants (Bergmann et al. 2015, Kartzinel et al. 2019). A wide scale application of these novel methods in the study of foraging ecology of Europe's diverse and rapidly changing ungulate communities should make it easier to draw strong conclusions about the effects of these communities on the individual species and on the landscapes that they inhabit and share with humans.

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.m905qftz9>> (Spitzer et al. 2020).

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Supplementary material (available online as Appendix oik-07435 at <[www.oikosjournal.org/appendix/oik-07435](http://www.oikosjournal.org/appendix/oik-07435)>). Appendix 1.