# Trophic resource use and partitioning in multispecies ungulate communities

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# Trophic resource use and partitioning in multispecies ungulate communities


## Abstract

Over the past decades, ungulates across the northern hemisphere have been expanding in range and numbers. This has raised concerns about their impacts, particularly on shared resources with humans, e.g., timber trees. Understanding how different ungulate species use trophic resources is therefore a crucial component of managing their populations.

In this thesis, I synthesized data from the literature and used faecal DNA metabarcoding to investigate diets and patterns of resource partitioning for ungulate communities in Sweden and at the European scale. I also evaluated the reliability of dung morphometry for identifying ungulate species. I found that species identification of faecal pellets is difficult where similar-sized ungulates coexist which questions the reliability of pellet counts as a monitoring technique in such systems. Dung morphometry could, however, clearly distinguish moose from the smaller deer species. Across Europe, average diets of the four main deer species fit well with predictions by Hofmann's hypothesis of ruminant feeding types. Red and fallow deer (mixed feeders) showed larger dietary plasticity than moose and roe deer (browsers). In Sweden, red and fallow deer adopted a more browser-like diet with high proportions of woody plant species in their diet. Dietary niche width was lowest for moose and highest for fallow deer but varied only little across seasons. Ericaceous shrubs like *Vaccinium* spp. comprised a major component in the diet of all four deer species. Intraspecific dietary overlap for moose was higher than dietary overlap with either of the smaller deer species. Moose diets also contained larger proportions of Scots pine *Pinus sylvestris* than those of the other deer species. In areas with high densities of the smaller deer, moose, but not the other deer species, consumed more pine and less *Vaccinium* spp. Feeding competition from the smaller deer species over *Vaccinium* spp. may drive moose towards increased browsing on pine, thereby exacerbating the forestry-moose conflict.

For the mitigation of this conflict, managing important food items like *Vaccinium* spp. and the populations of smaller deer species may be of equal or greater importance than a simple reduction in the number of moose.



*Keywords:* DNA metabarcoding, ungulates, dung morphometry, dietary overlap, resource partitioning, multispecies management, moose *Alces alces*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, fallow deer *Dama dama*



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# Utnyttjande av födoresurser i flerartssystem av klövvilt


## Sammanfattning

Under de senaste decennierna har stammarna av klövvilt vuxit på norra halvklotet, samtidigt som arterna utökat sina utbredningsområden. Parallellt har oron för negativa effekter av klövvilt ökat. Kunskap om hur olika klövvilt utnyttjar tillgängligt foder är central för att kunna förvalta klövviltstammar i förhållande till varandra och till jord- och skogsbruk.

I den här avhandlingen har jag undersökt vad älg, rådjur, kronhjort och dovhjort äter under året i olika typer av landskap i Sverige och Europa, och hur hjortarterna påverkar varandra genom sina foderval. Jag kombinerar litteraturstudier om europeiska klövviltsdieter med egna analyser av DNA-rester i viltets spillning för att generera kunskap om foderutnyttjande i olika klövviltssamhällen. Med DNA-metoder visar jag också att bestämning av arttillhörighet vid spillningsinventeringar är svårt när djurarterna har liknande kroppsstorlek, men att det är möjligt att skilja spillning från älg och från våra mindre hjortvilt.

Litteraturen visar att dieterna för Europas fyra huvudsakliga hjortvilt överensstämmer väl med Hofmanns hypotes om idisslartyper. Kron- och dovhjort (selektiva blandätare) visade större flexibilitet i sina foderval jämfört med rådjur och älg (kvistbetare). Enligt mina DNA analyser utnyttjade svenskt kron- och dovvilt en större andel vedartad växtlighet än vad de gör i Centraleuropa. Nischbredden på dieten var lägst för älg och högst för dovhjort, med liten variation mellan säsongerna. Älgens diet skiljde sig från de övriga hjortarna, som hade mer överlappande dieter. Ris av släktet *Vaccinium* (blåbär, lingon, odon) utgjorde en stor andel av födan för alla fyra hjortarter som undersöktes. Tall, *Pinus sylvestris*, utgjorde dock bara vanlig föda för älg. I områden med höga tätheter av de mindre hjortarterna åt älgen mindre *Vaccinium* och mer tall, medan motsvarande mönster saknades för de mindre arterna.

Detta antyder att födokonkurrens kan tvinga älgen att utnyttja tall i större utsträckning och därmed orsakar större konflikter med skogsbruket. För att minska dem kan det vara mer effektivt att förvalta viktiga foderarter och de mindre hjortarna, än att enbart fokusera på att reglera älgstammen.



*Nyckelord:* DNA metabarcoding, klövvilt, spillning, dietöverlapp, resursutnyttjande, flerartsförvaltning, älg *Alces alces*, rådjur *Capreolus capreolus*, kronhjort *Cervus elaphus*, och dovhjort *Dama dama*



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# Dedication

To you, dear reader.

*“Exactly!" said Deep Thought. "So once you do know what the question actually is, you'll know what the answer means.”*

Douglas Adams

The Hitchhiker’s Guide to the Galaxy

# Contents

# List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Spitzer, R.*, Felton, A., Landman, M., Singh, N.J., Widemo, F., Cromsigt, J.P.G.M. A dietary view on Europe's ungulate revival: Applying Hofmann's ruminant diversification hypothesis to 50 years of ungulate diets in Europe. (manuscript)

II Spitzer, R.*, Churski, M., Felton, A., Heurich, M., Kuijper, D.P.J., Landman, M., Rodriguez, E., Singh, N.J., Taberlet, P., van Beeck Calkoen, S.T.S., Widemo, F., Cromsigt, J.P.G.M. (2019). Doubting dung: eDNA reveals high rates of misidentification in diverse European ungulate communities. *European Journal of Wildlife Research*, 65:28

III Spitzer, R.*, Felton, A., Landman, M., Singh, N.J., Widemo, F., Cromsigt, J.P.G.M. Patterns of trophic resource use and partitioning along gradients of land-use and deer density in a Swedish multi-species ungulate community. (manuscript)

IV Spitzer, R.*, Coissac, E., Felton, A., Fohringer, C., Landman, M., Singh, N.J., Taberlet, P., Widemo, F., Cromsigt, J.P.G.M. Small shrubs with large importance? Competition over *Vaccinium* spp. might drive resource partitioning between moose (*Alces alces*) and smaller deer in a Swedish multi-species ungulate system. (manuscript)



* Corresponding author.

The contribution of Robert Spitzer to the papers included in this thesis was as follows:

I Designed the study with the co-authors, carried-out the data collection and analyses, and had main responsibility for writing.

II Came up with the idea, coordinated and participated in the fieldwork, performed the DNA extractions, participated in the PCR and bioinformatics, carried-out the statistical analyses and wrote the manuscript with contributions by co-authors.

III Developed the study with the co-authors, coordinated and participated in the fieldwork, performed the DNA extractions, participated in the PCR and bioinformatics, carried-out the statistical analyses and had main responsibility for writing.

IV Contributed to forming the idea, coordinated and participated in the fieldwork, performed the DNA extractions, participated in the PCR and bioinformatics, carried-out the statistical analyses and had main responsibility for writing.

# Abbreviations

| | |
|---|---|
| bp | Base pairs (in a DNA molecule) |
| DNA | Deoxyribonucleic acid |
| DNW | Dietary niche width |
| eDNA | Environmental DNA |
| EMBL | European Molecular Biology Laboratory |
| FOO | Frequency of occurrence |
| IUPAC | International Union of Pure and Applied Chemistry |
| LMH | Large mammalian herbivores |
| MOTU | Molecular operational taxonomic unit |
| NCBI | National Center for Biotechnology Information |
| NMDS | Non-metric dimensional scaling |
| PCR | Polymerase chain reaction |
| RRA | Relative read abundance |
| V | Intraspecific dietary variation |

# 1 Introduction

## 1.1 Decline and recovery of ungulates in the northern hemisphere

Ungulates or 'hoofed animals' account for the vast majority of large mammalian herbivores on earth today. They have evolved into a striking number of species and their influence stretches across nearly every terrestrial biome (Putman, 1996), with the exception of Antarctica.

Interactions between ungulates and humans arose early. Ungulates feature prominently in some of the earliest human art such as the cave paintings in Chauvet-Pont d'Arc, France, from ca. 35,000 years ago (Quiles *et al.*, 2016) and the resources obtained from hunting wild ungulates were central to the meat-based subsistence of Paleolithic cultures (Chahoud *et al.*, 2016). Recent evidence suggests that humans were capable of overexploiting populations of wild animals (including ungulates) already during prehistoric times and may have been the driving force behind numerous megafaunal extinction events (Sandom *et al.*, 2014; Araujo *et al.*, 2017), a trend that unfortunately continued into more recent times.

About 400 years ago, the arrival of European settlers in North America heralded dramatic declines of many wildlife species. While exact pre-settlement population sizes of big game are not known, estimates placed numbers up to 10 times higher than even today (Krausman & Bleich, 2013). The reduction of American bison (*Bison bison*) from once tens of millions to near extirpation by the end of the 19$^{th}$ century (Shaw, 1995) has become perhaps one of the most infamous examples of wanton, industrial-scale overexploitation of an iconic species. Populations of smaller ungulates like white-tail deer (*Odocoileus virginianus*) or mule deer (*Odocoileus hemionus*) also rapidly declined. Although overhunting was often the most apparent cause in the demise of wild

ungulates, the problem went deeper and became more complex when settlers introduced a broad range of domestic herbivores and started to reshape the landscape to suit their livestock husbandry and farming practices (Vavra & Riggs, 2010). Native ungulates that had adapted to stochastic environments shaped by climatic extremes and a range of natural disturbance patterns such as fire, found themselves increasingly faced with ecologically incomplete, compressed, and homogenized habitats (Vavra & Sheehy, 1996; Vavra & Riggs, 2010).

The story of North American wildlife after European arrival in many ways reflects the history of large herbivores in Europe itself. Prior to the domestication of livestock, wild ungulates used to be a crucial source of protein (Gordon, 2009). During the rise of agrarian societies and later the industrial revolution, large parts of the European landscape underwent intense transformations into agricultural fields or grazing pasture while the remaining forests were exploited for timber, firewood, and charcoal (Deinet *et al.*, 2013). Growing numbers of people coupled with improved hunting techniques led to complete or local extinctions of ungulate species like the aurochs (*Bos primigenius*) in 1627 (Stokstad, 2015), the European bison (*Bison bonasus*; except for a few individuals in captivity - Krasinska and Krasinski (2007)), and the wild boar (*Sus scrofa*) in Sweden (Hagström *et al.*, 2010).

According to the World Wildlife Fund (2016), half the planet's wildlife populations have declined since 1970. This trend, however, is not homogenous across regions and species (Francesco *et al.*, 2018). In fact, throughout the northern hemisphere, ungulates have become a notable exception and shown a remarkable recovery over the past decades (Cote *et al.*, 2004). In North America, intensive conservation efforts have brought species like bison or pronghorn (*Antilocapra americana*) from the verge of extirpation back to sizable populations of approximately 500,000 (Krausman & Bleich, 2013) and 750,000 (IUCN SSC Antelope Specialist Group, 2016), respectively. The numbers of several deer species, such as mule deer and white-tailed deer, have also recovered to such an extent that they are now perceived as overabundant in some regions (Cote *et al.*, 2004; Pendergast *et al.*, 2016). Similarly, Europe has seen strong increases in several deer species since the 1960s (Figure 1); moose (*Alces alces*) have increased by approximately 200%, roe deer (*Capreolus capreolus*) by 250%, and red deer (*Cervus elaphus*) by 400% (Deinet *et al.*, 2013). Across the northern hemisphere, ungulates have benefitted from increased protection and reduced exploitation, the widespread absence of large carnivores, and the decline of free-ranging livestock coupled with land abandonment due to urbanization (Cote *et al.*, 2004; Deinet *et al.*, 2013). Moreover, new agricultural and silvicultural practices like the sowing of winter wheat or plantation forestry

have created abundant food sources while reintroduction programs and less severe winters further promoted increases in population sizes and expansions of species' ranges (Cote *et al.*, 2004; Deinet *et al.*, 2013). The result are the formation of novel communities inhabiting landscapes that are heavily altered by humans and with species compositions that have no historic reference, i.e., novel ecosystems (Hobbs *et al.*, 2009; Morse *et al.*, 2014).

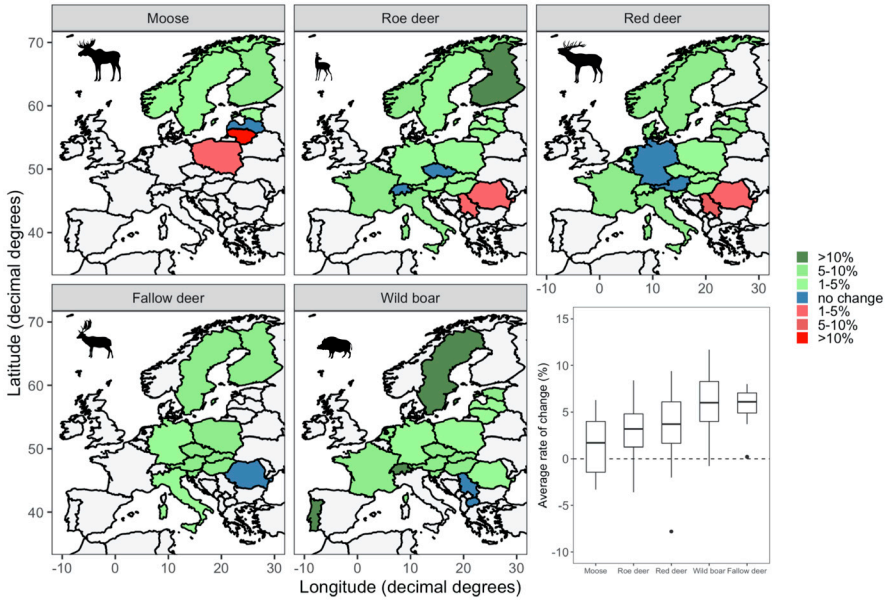


*Figure 1.* Average rates of change at country level for populations of five European ungulate species. The colours indicate increases (green), decreases (red), no change (blue), and no data (grey). Data were extracted for all available years from 1965 to 2007 from graphs and tables published in Apollonio and Andersen (2010); the figure is based on data compilation by Söder (2017). Estimates are based on bag statistics (hunting records) except for Italy and the Netherlands, where they reflect population censuses. Species-level variation is summarized by the boxplots (bottom right).

While high abundances of ungulates are often favoured through economic incentives from hunting (Gordon *et al.*, 2004), there are also serious concerns about their environmental and socio-economic impacts (Weisberg & Bugmann, 2003; Cote *et al.*, 2004). Ungulates can exert enduring effects on the habitats and resources they utilize (Frank *et al.*, 2000; Palmer *et al.*, 2004; Wolf *et al.*, 2007). Through their impact on vegetation, ungulates influence ecosystem processes like nutrient cycling and energy flow (Hobbs, 1996) and can have cascading effects on other wildlife such as birds (Mathisen & Skarpe, 2011; Carpio *et al.*, 2014a) or invertebrates (Carpio *et al.*, 2014b; Moe *et al.*, 2018). Conflicts between humans and ungulates can arise through negative impacts on shared

resources such as damage to crops and timber trees (Bleier *et al.*, 2012), collisions with vehicles (Björnstig *et al.*, 1986), or through the transmission of diseases to livestock (Martin *et al.*, 2011) and humans (Ostfeld *et al.*, 2006). Rising ungulate numbers, and species that are expanding their ranges may change the competitive interactions within ungulate communities. This may also affect human interests, for example, when the species that are favoured by hunters are also the ones that are most negatively affected by increased competition.

These aspects become especially relevant in the context of novel ecosystems as there are no historical analogues for reference. We currently lack an understanding of how the novel ungulate communities and landscapes influence the interactions and coexistence of species in these communities. Investigating these questions is therefore of crucial importance.

## 1.2 Trophic resource use and partitioning by ungulates

The mechanisms that facilitate coexistence between sympatric species are complex, but it has been generally accepted that coexistence between large herbivores is rooted in the competitive exclusion principle (Hardin, 1960). Under this principle, natural selection favours the separation of ecologically similar species (Pianka, 1988); i.e., potential competitors can only coexist if they inhabit different realized niches. Such niches can be created through utilization of different resources or via separation in time and space. For ungulates, forage partitioning has widely been suggested as the main mechanism underlying their coexistence (Putman, 1996; Kirchhoff & Larsen, 1998; Mysterud, 2000; Bertolino *et al.*, 2009) although predation pressure (Sinclair, 1985; Sinclair *et al.*, 2003) and disease susceptibility (Dobson & Hudson, 1986; Escobar *et al.*, 2019) may also be important.

Food is one of the basic prerequisites for life. Meeting their nutritional and energetic requirements is thus one of the strongest drivers of animal behaviour. All ungulates experience energy-demanding annual cycles of reproduction and lactation, as well as periods of nutritional deprivation and climatic stress (Vavra & Riggs, 2010). Their diet (the quantity, composition and quality of ingested foods) therefore directly affects condition and survival of individuals. This ultimately also influences the fitness and population dynamics of species, as well as their environmental and economic impacts (Holá, 2016). To cope with such challenges, ungulates have evolved a suite of morphological characteristics which govern the type of landscape and resources each species can efficiently exploit to meet its nutritional demands (Vavra & Riggs, 2010) while simultaneously minimizing competition with other species.

Ecologists have long been aware that different species of large herbivores appear to favour different types of forage. Inspired largely by observations of complex African herbivore communities (e.g., Van Zyl (1965), Jarman (1971)) a distinction was initially made between browsers (diet dominated by woody and non-woody dicotyledons) and grazers (diet dominated by graminoids). Hofmann and Stewart (1972) realized the insufficiency of this dichotomy and introduced intermediate or 'mixed' feeders (diets composed of both browse and grass) as a third feeding type. Focussing on ruminants, they explained resource partitioning between large herbivores and the emergence of different feeding types as evolutionary adaptations in digestive morphology.

According to this ruminant diversification hypothesis (Hofmann, 1989), browsers (which Hofmann termed 'concentrate selectors') are well adapted to digest dicotyledons which are relatively rich in protein and soluble cell contents. However, due to higher lignin content and the presence of protective plant secondary compounds (e.g., tannins), the overall digestibility of browse tends to be lower than that of graminoids (Clauss *et al.*, 2008). Grasses (which represent the majority of graminoids) are an evolutionarily younger food source than browse; extensive grasslands only emerged within the past 25 million years during the later Cenozoic (Janis, 2008; Strömberg, 2011). The first true grazers entered the scene as recently as 10 million years ago whereas the first ungulates date back to 55 million years ago (Janis, 2008). This is why browsing is sometimes viewed as the more primitive form of ungulate foraging (Bodmer & Ward, 2006). Grazers are better adapted than browsers to utilize the thick ('fibrous') cell walls of grasses that consist mostly of slowly digestible cellulose (Hofmann, 1989). Compared to browsers, grazers tend to have a larger foregut and wider muzzles which promotes the bulk intake and digestion of grasses rather than browse. For a relative comparison of the digestive anatomy between grazers and browsers see Shipley (1999).

Hofmann (1989) strongly suggested that the morphophysiological adaptations of the different feeding types were essentially independent of body size. This has repeatedly been questioned by later authors (Gordon & Illius, 1994; Gordon & Illius, 1996). These studies found that after controlling for body size, there appeared to be little difference in the digestive efficiency between browsers and grazers. But why should body size be linked to digestive efficiency?

Larger bodies are better at retaining heat due to decreasing surface-to-volume ratios. This relationship underlays the biological principle known as Kleiber's law (Kleiber, 1932), which states that an animal's basal metabolic rate scales to the 0.75 power of its mass. This means that larger animals have relatively slower metabolisms than small ones (i.e., mass-specific metabolic rate decreases with

body mass). Several studies have shown that food intake (measured as absolute dry matter) in mammalian herbivores scales similarly to Kleiber's law (Bourliere, 1975; Kirkwood, 1983; Shipley *et al.*, 1994) whereas gut volume increases as a constant proportion of body mass (Parra, 1978; Demment, 1982). This means that with larger body mass the volume of the gastrointestinal tract increases relative to absolute intake requirements which then allows for longer retention times and a more thorough fermentation of ingesta (Bell, 1971; Jarman, 1974; Demment & Van Soest, 1985). Simply put, smaller herbivores with high mass-specific metabolic rates require energy-rich, high-quality foods whereas large herbivores can tolerate lower-quality forage - the Jarman-Bell principle (Bell, 1971; Geist, 1974; Jarman, 1974). Food quality in these studies refers to digestibility. The latter was defined as the ratio between easily digestible cell components like proteins and poorly digestible, fibrous cell walls rich in cellulose. Low quality food can thus be characterized by a low protein-to-fibre ratio (Cromsigt, 2006) although the components and drivers of what constitutes a 'high quality diet' are complex and still being debated (see Felton *et al.* (2018) for a review).

Since grasses are more fibrous than browse the Jarman-Bell principle may explain, at least in part, why grazing ruminants on average are larger than browsers (Bell, 1971; Bodmer, 1990; Perez-Barberia & Gordon, 2001) although notable exceptions like the giraffe (*Giraffa camelopardalis*) exist. The Jarman-Bell principle suggests that scaling of body size facilitates trophic resource partitioning between large herbivores for the sake of energetic efficiency (Bell, 1971; Austin *et al.*, 1983; Sheehy & Vavra, 1996). Such a differentiation in body size is indeed common among coevolved, ecologically similar species (MacFadden & Shockey, 1997). While some aspects of resource partitioning between the different ruminant feeding types currently still remain unresolved (Clauss *et al.*, 2008), it appears that body size might be mostly linked to nutrient demand, while morphological characteristics of the gut and mouth influence selectivity (Shipley, 1999).

Irrespective of what ultimately drives resource partitioning between large herbivores, such partitioning is almost never complete as numerous studies on trophic resource overlap have shown. For example, Kirchhoff and Larsen (1998) reported a dietary overlap between elk (*Cervus elaphus roosevelti*) and sitka black-tailed deer (*Odocoileus hemionus sitkensis*) of 64% during winter in Alaska. During summer in Colorado, dietary overlap between elk and mule deer was 32%, and 42% between elk and cattle (*Bos taurus*) (Hansen & Reid, 1975). In European studies, substantial dietary overlap between ruminants of different feeding types has also been observed. In northern Fennoscandia, Mysterud (2000) found dietary overlaps between moose and roe deer of 21-34%, between

moose and red deer 32%, between red deer and sheep (*Ovis aries*) 59-64%, between sheep and goat (*Capra hircus*) 77%, and finally 55% between sheep and reindeer (*Rangifer tarandus*). In the New Forest of England, dietary overlap between fallow deer (*Dama dama*) and cattle decreased from 98% during spring to 72% in winter whereas for fallow deer and roe deer dietary overlap increased from 33-66% during the same period (Putman, 1996). The functional significance of dietary overlap and other interactions between large herbivores does not, however, hinge on the fact that they occur, but rather on whether they are competitive, neutral, or facilitative in nature (Vavra & Riggs, 2010). To determine which is the case, resource use and population dynamics in multi-species ungulate communities must be regularly monitored with reliable tools.

An improved understanding of trophic resource use and partitioning will help in predicting what deer species eat under different conditions which in turn is crucial for steering the management of deer populations in the light of human-deer conflicts. The incorporation of such knowledge will aid in reducing the uncertainty associated with the management of natural systems and forms an integral part of the adaptive management process (Fontaine, 2011).

## 1.3 Objectives

With this thesis I aim to contribute to the existing knowledge about how ungulates use and partition trophic resources. Set within the dynamic context of emerging novel multi-species ungulate communities in Sweden, my research focusses primarily on four deer species that are of high ecological and economic interest: moose, roe deer, red deer, and fallow deer. Using various methods, especially DNA metabarcoding, I investigate how these species utilize trophic resources in anthropogenically modified landscapes. I attempt to provide insight into the complex processes that shape the intra- and interspecific relationships in multispecies ungulate communities.

It is my hope that the findings presented here will be informative not only to ecologists but also to managers and the general public in the joint effort to assure a sustainable future for our northern landscapes in which both humans and wildlife are allowed to thrive.

Specifically, my objectives were to:

1. Synthesize our current understanding of European ungulate diets and resource partitioning patterns in the light of Hofmann's ruminant diversification hypothesis at the European scale (Paper I)

2. Use DNA metabarcoding on environmental DNA (eDNA) samples (i.e., faecal pellets) to improve monitoring of multispecies ungulate systems. Two key components of this objective were to quantify ungulate species misidentification rates of pellet groups (Paper II) and to characterize diets (Papers III & IV).

3. Investigate patterns of trophic resource use and partitioning among deer species along gradients of land-use and deer density (Paper III)

4. Investigate how resource partitioning between moose and smaller deer species may affect the moose-forestry conflict (Paper IV)

# 2 Materials and Methods

## 2.1 Study area and species

Except for Paper I, which was based on data at a European scale extracted from the literature, most of the data for this thesis (Papers II-IV) originated from two Swedish sites, Nordmaling and Öster Malma (Figure 2a). The northern part of the study area (Nordmaling) is located in the boreal forest while the southern part (Öster Malma) extends into the boreal-to-nemoral transition zone. Both sites are situated in landscapes that have been modified by humans and are characterized by a mosaic of forests, mires and agricultural land. The scale and intensity of agriculture increases along a north-to-south gradient, but the proportion of arable land typically does not exceed 50%. Most agricultural fields range from one to 10 hectares in size with the average being approximately four hectares (A. Widén, personal communication, October 22, 2019). Common agricultural practices are animal husbandry and the growing of cereals, root vegetables and fodder with leys typically comprising 40-70% of the fields at the Öster Malma site (Åberg, 2016). Forestry is largely practiced as a rotational system of clear-cutting and replanting. Pre-commercial thinning is widely applied to young stands. Common tree species throughout the study area include Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), birch (*Betula* spp.), poplar (*Populus* spp.), and willows (*Sali*x spp.). At the Öster Malma site, oak (*Quercus* spp.) is also common. The forest field layer is typically dominated by ericaceous shrubs like bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), or heather (*Calluna vulgaris*), as well as various grasses, mosses and lichens.

Each study site possessed an already established sampling grid consisting of 76 square 1x1km transects in Nordmaling and 50 in Öster Malma (Figure 2b,c) which, initially, formed part of a continuous environmental monitoring program

(FOMA, 'Fortlöpande miljöanalys', Edenius (2012)). On average, transects were spaced 3-6 kilometres apart, measured between the centres of the 1x1km blocks. Each transect contained 16 evenly spaced sampling plots (four on each side, 200m apart) for the annual ungulate pellet group counts (Figure 2d).

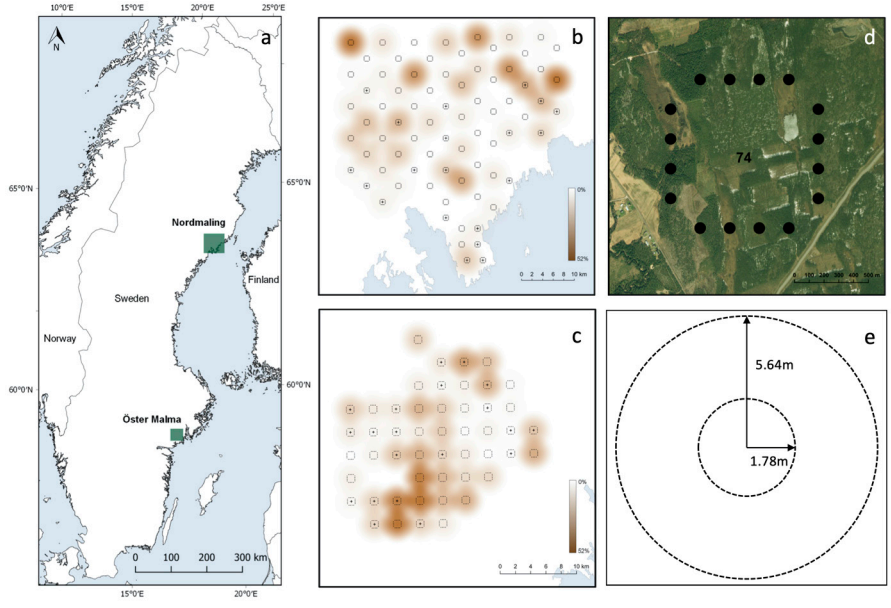


*Figure 2.* Location of the two study sites, Nordmaling and Öster Malma in Sweden (a). Each study site contained a grid of 1x1km transects; 76 in Nordmaling (b) and 50 in Öster Malma (c). Most transects were sampled only during the spring pellet group counts; a subset of 20 transects at each site (indicated by a dot at the centre) was sampled on a bi-monthly basis. The brown shading corresponds to the proportion of agricultural land (0-52%). Each transect contained 16 evenly-spaced sampling plots for pellet group counts (d). At each plot, pellet groups were counted on $100m^2$ (r = 5.64m) or $10m^2$ (r = 1.78m), depending on species and site (e). (from Paper III)

Moose, roe deer, red deer, and fallow deer occur sympatrically at both sites (Appendix 1d). The first three deer species have always been considered part of the Swedish fauna although red deer historically did not occur as far north as the Nordmaling study site. This Nordmaling population originated from animals that escaped from enclosures during the 1980s and have since become well established (Fahlgren & Lodestål, 2011). Fallow deer are historically a species from southern Europe and Turkey. They were introduced to Sweden in the 16$^{th}$ century and have become a firmly established species, especially in southern Sweden (Hagström *et al.*, 2010). Since 1988, fallow deer have officially been considered a part of the native fauna (Länsstyrelsen Södermanland, 2014). Further details about the four deer species are provided in Table 1. Other ungulates that occur in the study area are wild boar in Öster Malma and, in

Nordmaling, reindeer which sporadically occur during the winter. Historically, reindeer was a wild species in Sweden but their domestication intensified during the 15th and 16th century and they are now considered to be domesticated (Bjørnstad *et al.*, 2012). Large carnivores are represented by lynx (*Lynx lynx*) at both sites and brown bear (*Ursus arctos*) in Nordmaling. Wolves (*Canis lupus*) are currently still absent from the study area.

Apart from the Swedish locations, Paper II also included samples from four additional European sites, namely Kraansvlak (Zuid-Kennemerland National Park, Netherlands), Maashorst (Netherlands), the Bavarian Forest National Park (Germany), and the Białowieża National Park (Poland).

Table 1. *Short profiles of the four deer species studied for this thesis. The information is based on Hagström et al. (2010) unless otherwise indicated. (MBH = Maximum browsing height, CP = Calving period, NO = Number of yearly offspring). The mass in square brackets indicates the average adult slaughter weight (approximately 55% of live weight) in Sweden (Wiklund & Malmfors, 2014).*

| Common name | Scientific name | Mass (kg) | MBH[a] (m) | Rut | CP | NO | Sociality | Feeding type[b] |
|---|---|---|---|---|---|---|---|---|
| Moose | *Alces alces* | 200-500 [168] | 3 | Sep/ Oct | May/ Jun | 1-2 | Solitary, occasionally in groups during winter | Browser (CS) |
| Roe deer | *Capreolus capreolus* | 20-30 (males slightly heavier) [13.5] | 1.5 | Jul/ Aug | May/ Jun | 2 | Solitary, males are territorial | Browser (CS) |
| Red deer | *Cervus elaphus* | max. 150 (females) to 250 (males) [75] | 2.3 | Aug/ Sep | May | 1 | Single-sex herds, mature males gather female groups (harems) during the rut | Mixed feeder (IM) |
| Fallow deer | *Dama dama* | 50-70 (females), 90-130 (males) [32] | 1.8 | Oct/ Nov | Jun/ Jul | 1 | Large single-sex groups of up to 70 individuals, males often solitary during the rut | Mixed feeder/ grazer (IM/GR) |

a) Nichols et al. (2015)

b) The classification of feeding types is based on Hofmann (1989) but the more broadly used names in today's literature have been adopted. Hofmann's original denotations are given in parentheses; CS = Concentrate selector, IM = Intermediate types, GR = Grass/roughage eaters.

## 2.2 Study designs and rationale

### 2.2.1 Ungulate diets across Europe (Paper I)

From the European literature of the past five decades (1965-2016), I extracted records of fully quantified diet compositions of moose, roe deer, red deer, fallow deer, and wild boar. Wild boar (a hindgut fermenter) was included as a contrast to the ruminant deer species in some of the analyses. I then used these diet data to investigate five hypotheses based on Hofmann's classification of ruminant feeding types:

1. Ruminants separate mainly along a browser-to-grazer continuum with mixed feeders showing larger variation than browsers.
2. Wild boar diet is distant from deer diets even in the context of shared food categories, i.e., plants.
3. Browser diets are less variable across habitat types than those of mixed feeders.
4. Browsers show higher intraspecific dietary overlap than mixed feeders.
5. Interspecific diet overlap is highest in winter when the variety of available food is lowest. Similarly, the magnitude of seasonal changes in dietary overlap should be lowest in southern Europe where seasonal changes in vegetation are the least severe.

The literature on the dietary ecology of European ungulates is extensive but the myriad of analytical methods, diet classification schemes, and the variation in spatial or temporal extent of studies, have made comparisons difficult. My aim, therefore, was to consolidate ungulate diets from across Europe to facilitate investigations of intra- and interspecific use and partitioning of trophic resources on a continental scale. Paper I also serves as a framework and reference for the research directed at the Swedish and other European multi-species ungulate communities in subsequent studies.

### 2.2.2 (Mis)identification of ungulate dung (Paper II)

Assigning ungulate faecal pellets to the correct species is crucial for monitoring techniques like pellet group counts or any other research relying on ungulate pellets, including my own diet studies. However, the reliability of visual cues for species identification of ungulate pellets has frequently been questioned (Alvarez, 1994; Bowkett *et al.*, 2013; Yamashiro *et al.*, 2013). To quantify species misidentification rates, I compared the field identification of faecal

samples (Field ID) with DNA verified results (DNA ID). Faecal samples were collected from different multi-species ungulate communities (comprising a total of nine ungulate species) at six sites in four European countries (Figure 1 in Paper II). Field ID was assigned by local observers and DNA ID determined through DNA metabarcoding. On a subset of the samples from the Swedish study sites, I also tested the effect of dung morphometry, observer experience, and season on species identification success.

### 2.2.3 Trophic resource use and partitioning (Paper III)

I used faecal DNA metabarcoding to characterize diet composition and the partitioning of trophic resources among four deer species (moose, roe deer, red deer, and fallow deer) in Sweden. As a first step, I compared how the diet composition revealed by metabarcoding compared to the diets predicted by Hofmann's classification of feeding types and also provided diet summaries at different taxonomic resolutions for each of the four species. I then investigated the effects of season, habitat diversity, the proportion of arable land, and overall ungulate density on dietary niche width (DNW) and dietary overlap. Combining field measurements of food availability with diet data enabled me to assess selectivity for major food items. The latter included commercially valuable timber species like pine and spruce which are frequently found at the centre of the forestry-ungulate conflict. An improved understanding of the drivers behind ungulate food choices and resource partitioning forms a crucial component of mitigating this conflict.

### 2.2.4 Trophic resource competition (Paper IV)

Paper III had shown that ericaceous shrubs (*Vaccinium* spp.) in the forest understory represent an important food source for all four deer species throughout the year. Studies on African ungulate communities have demonstrated that feeding competition with smaller species might replace larger species from the field layer and drive them towards higher foraging strata that offer larger bites (Cameron & du Toit, 2007). Using data on diet composition (obtained by faecal DNA metabarcoding) and an index of deer densities, I tested the hypothesis that feeding competition over *Vaccinium* spp. from the smaller deer (roe, fallow, and red deer) in the field layer might push moose towards greater consumption of pine which is generally also found at higher foraging strata. This hypothesis of bite-size driven partitioning of feeding heights (Woolnough & du Toit, 2001) was tested for two seasons, spring and winter. The winter analysis was based on a subset of 32 transects in the study area on

which I had measured food availability and snow depth. This allowed me to test the effect of these two variables (in addition to deer density) on pine and *Vaccinium* spp. consumption by moose. For the much larger spring dataset, comprising all 126 transects in the study area and dung collections from three years (2015-2017), I could only assess the effect of deer density as no food availability measurements had been carried-out on the vast majority of transects. Pine is the most commercially important timber species in Sweden and the forestry-ungulate conflict currently largely corresponds to moose impacts on pine. Understanding the drivers of pine browsing as holistically as possible is therefore of crucial importance, especially in the context of emerging novel ungulate communities.

## 2.3 Data collection

### 2.3.1 Literature review (Paper I)

I 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*). I then manually screened the results for studies that were carried-out in European ungulate systems (with the exception of the Russian Federation) and contained fully quantified diet compositions for any of the five species. A further filtering criterion was that the research had been conducted on free-ranging animals.

To account for the differences in taxonomic resolution of diet profiles used among authors, I standardized diets into 11 main categories which provided the best overlap across studies (Supporting Information S1 in Paper I). If studies contained repeated measurements for the same location (e.g., winter diets for several years), I averaged the reported values to confer equal weights to the different studies. When seasons were reported, I kept the classification used by the authors. If data was presented on a monthly scale, I used the meteorological seasons for the northern hemisphere (Deutscher Wetterdienst) and averaged diets accordingly. I also recorded habitat type and geographic location.

### 2.3.2 Collection and storage of faecal samples (Papers II-IV)

The following description pertains only to the faecal samples collected in Sweden. The collection and storage methods for the samples collected at the other four European locations, which were not included in the diet analyses for this thesis, followed similar protocols and are detailed in Paper II.

Fresh faecal pellets from moose, roe deer, red deer, and fallow deer were collected along the whole length of the 1x1km square transects (= 4km / transect) at both study sites. Dung samples from wild boar and reindeer were also collected but not included in the diet analyses in this thesis due to small sample size, irregular occurrence and only partially resolved diet composition due to marker limitations (see section 3.5). They were, however, included in the species misidentification study (Paper II). Samples were considered fresh if they still had a wet, shiny surface and showed no signs of infestation by coprophages (Hemami & Dolman, 2005).

Sample collections were carried-out each year from 2015 to 2017 on all transects as part of the annual pellet group counts (see section 2.3.4) in spring just after snowmelt (Öster Malma: March-April, Nordmaling: May-June). On a subset of 40 transects (20 at each study site, Figure 2b,c) selected to capture gradients in the proportion of arable land and ungulate densities, faecal samples were also collected on a bi-monthly basis (i.e., alternatingly on 20 of the 40 transects each month) from September 2016 until November 2017. Because not all of these transects were accessible during all months, the number of transects included in the analyses can vary slightly between studies (e.g., 32 transects in Paper IV). We aimed at collecting five samples for each deer species per transect and visit. To minimize the risk of pseudoreplication and maximize the chance of sampling different individuals, we placed at least 200m between samples from the same putative species.

For DNA analysis, approximately 2g of fresh faeces were placed into sterile, airtight scintillation tubes (20mL) filled with silica gel desiccant (~ 1-3mm, with indicator [orange], Merck KGaA, Germany) (DeMay *et al.*, 2013; Taberlet *et al.*, 2018). We used disposable plastic spoons or nudged faecal pellets directly into the collection tube while carefully avoiding contact with other samples or the collector to prevent contamination. The silica-dried samples were then stored in the dark at room temperature until further processing.

### 2.3.3 Dung morphometry (Paper II)

Morphometric measurements (length and width) were taken on five randomly selected faecal pellets (Hasler & Senn, 2012) from fresh pellet groups of moose, roe deer, red deer, fallow deer, and reindeer during sample collections between March and June 2017. Measurements were averaged for each pellet group (Woodruff *et al.*, 2016) and we also counted the number of pellets in each group. Species identification was initially assigned by observers in the field and later verified through DNA analysis. To minimize the risk of contamination, we first collected pellets for DNA analysis before proceeding to the morphometric

measurements. Measurements were initially taken with precision callipers which proved to be impractical under field conditions. We therefore switched to photographing pellets on grid paper in the field, followed later by digital measurements using the free software Digimizer (version 4.6.1, available at www.digimizer.com). Before switching methods, I first used a test set of 50 pellets to confirm that measurement results did not significantly differ between methods.

### 2.3.4 Ungulate densities (Papers III & IV)

Ungulate pellet groups were counted annually in spring just after snowmelt on 16 evenly spaced sampling plots in each transect. The circular sampling plots consisted of 100 $m^2$ (r = 5.64 m) for counts of putative moose and red deer pellet groups and of 10$m^2$ (r = 1.78 m, same centre point) for roe and fallow deer (Figure 2e). From 2016 onwards, roe and fallow deer pellet groups were counted on 100 $m^2$ at the Nordmaling site due to the relatively low densities of these species at that site. In order to be included in the count, the centre of a pellet group had to be located within the plot boundaries. For a dung pile to be considered a pellet group, it had to consist of at least 20 individual pellets for moose and red deer or of 10 pellets for roe and fallow deer. Because plots were not cleaned between annual surveys, we counted only pellet groups that had been deposited after the leaf-fall of the previous autumn, i.e., pellet groups that were deposited above the leaf litter and not heavily decomposed. The dung counts therefore largely represented the winter and spring densities. Even prior to the results of Paper II we had suspected large overlaps in dung morphometry between ungulate species, particularly between roe and fallow deer. Field ID to putative pellet groups from these two species was thus assigned using thresholds suggested by Edenius (2012); fallow deer > 45 pellets/group, roe deer ≤ 45 pellets/group. Pellets group counts were standardized to the unit of pellet groups/1000$m^2$. Deer density classes were defined based on the quartiles of the deer density index as 'low' (< 2.0 pellet groups/1000$m^2$), 'medium' (2.0 – 28.8 pellets groups/1000$m^2$), and 'high' (> 28.8 pellet groups/1000$m^2$) (Paper IV). Transects on which less than 75% of the total plot area had been surveyed were excluded from further analyses.

In Paper IV, I was specifically interested in the effect of the smaller deer species on moose and therefore combined the densities of putative roe, red, and fallow deer into one deer density index. The ungulate density index in Paper III on the other hand refers to the density of all four deer species combined.

### 2.3.5 Habitat composition and food availability (Papers III & IV)

Habitat composition was extracted from the Swedish National Landcover database (Naturvårdsverket, 2019) using a radius of 1km from the centre of each transect. I excluded bodies of water from the final habitat composition since they do not represent deer habitat.

Food availability was measured during the bi-monthly collections of faecal samples on the same subset of transects. Because ungulates of different body size can forage at different heights and may therefore experience food availability differently, I classified foraging height strata for each deer species based on the maximum browsing heights reported by Nichols *et al.* (2015), see Table 1. I then recorded food availability for each of these strata at approximately every 40m along transects (= 100 measurements/transect) as vegetation hits on a 3.5m long pole, following the step-point method (Evans & Love, 1957; Coulloudon *et al.*, 1999). Hits were recorded according to 24 vegetation categories or as 'non-vegetation' (Appendix 1a). The recorded hits are analogous to potential bites on vegetation by foraging ungulates and can easily be converted to proportions which facilitates comparisons between food availability and diet composition. Snow depth (Paper IV) was measured with centimetre markings on the pole alongside the food availability measurements and averaged for each transect.

## 2.4 DNA metabarcoding

The use of non-invasively collected samples has been popular among wildlife ecologists due to their many advantages such as the comparatively easy and cost-efficient collection without the need of handling and stressing animals. Environmental DNA (eDNA) refers to the complex mixture of genomic DNA contained in different types of environmental samples (Taberlet *et al.*, 2012) such as soil, sediment, water, or faeces (Taberlet *et al.*, 2018).

To determine the taxa present in an eDNA sample, there are several options. If the research goal is to detect single species, quantitative PCR is a common approach (e.g., López-Andreo *et al.* (2012), Loh *et al.* (2014)). If the aim is to detect multiple taxa, as is usually the case in diet studies, DNA metabarcoding offers an increasingly popular alternative. The term DNA metabarcoding was first introduced by Pompanon *et al.* (2011) and refers to the simultaneous identification of numerous taxa in the same eDNA sample. A metabarcode corresponds to a short, taxonomically informative DNA region flanked by two conserved sites where primers anneal (Taberlet *et al.*, 2018).

After the collection of eDNA samples in the field, a DNA metabarcoding experiment typically consists of the steps described below, followed by the ecological interpretation of the results.

### 2.4.1 DNA extraction

Approximately equal amounts of dried dung (corresponding to 1 moose pellet or 2g) were crushed between folded-over pieces of aluminium foil, placed in 20mL scintillation vials and covered with 70%-ethanol. For thorough mixing and cell disruption, the vials were then placed for 90sec in an ultrasonic bath (Branson 2200). From the lysate, we pipetted 1800µL into 2mL microtubes and centrifuged for 10min at 13200rpm (16168 x g). After discarding the ethanol supernatant, 20µL of Proteinase K and 180µL of ATL buffer were added to the remaining pellet. Samples were then incubated for 30min at 56ºC, shaken every 10 minutes and centrifuged again for 30sec at 3.000rpm (835 x g). DNA purification was carried out to an elution volume of 100µL on a QIASymphony SP robot using the QIASymphony DSP DNA minikit (Qiagen, Hilden, Germany) according to the manufacturer's instructions.

### 2.4.2 DNA metabarcoding markers and PCR amplification

To allow for consistent PCR amplification, markers used in diet metabarcoding must be of sufficiently short length to account for the degradation typically encountered in eDNA samples (Valentini *et al.*, 2009). In our studies, we targeted two taxonomic groups: mammals and plants. To amplify mammalian DNA, we used the primer pair (Mamm02_F & Mamm02_R), which amplifies a 60 to 84-bp fragment of the mitochondrial 16S gene (Giguet-Covex *et al.*, 2014). To restrict amplification of possible contamination from human DNA, we used a blocking oligonucleotide. For plants, we chose the universal primer pair (Sper01_F & and Sper01_R) that amplifies the P6 loop of the trnL (UAA) intron of chloroplast DNA (Taberlet *et al.*, 2018). The Sper01 primers correspond to the g/h primers of (Taberlet *et al.*, 2007) and have been widely used for analysing degraded template due to the relatively short length of amplicons, ranging from 10 bp to 220 bp (mean: 48 bp), as well as good coverage and taxonomic resolution for the target group (Taberlet *et al.*, 2018). Further details and primer sequences are provided in Table 2. To assign sequence reads to the corresponding sample after high-throughput sequencing, we used 36 tags of eight nucleotides with at least five differences between each of them (available at www.oup.co.uk/companion/taberlet), which were added to the 5’ end of each primer. The resulting 36 different reverse primers and 32 forward primers

allowed for tagging of 1152 PCR products and controls (the equivalent of twelve 96-plates) in the same library. Tags were flanked on the 5' end by two to four random nucleotides (NN – NNNN) to improve detection of the different clusters on the sequencing surface, and to also improve base calling (Taberlet *et al.*, 2018). All PCR were carried out in a final volume of 20µL containing 2µL of DNA extract. For the Sper01 primer pair, the amplification mixture consisted of 10µL of AmpliTaq Gold® 360 master mix (Applied Biosystems), 0.5µM of each primer and 0.16µL (20 mg/mL) of bovine serum albumin (BSA, Roche Diagnostic). For the Mamm02 primer pair, the amplification conditions were the same, except that the primer concentrations were 0.2µM each, in the presence of a human blocking oligonucleotide at 2µM. Polymerase activation was performed at 95ºC for 10min, followed by 40 or 45 cycles for Sper01 and Mamm02, respectively, of 95ºC for 30sec (denaturation), 50ºC for 30sec (primer annealing) and 72ºC for 60sec (extension) with a final elongation for seven minutes at 72ºC at the end. We carried-out three PCR replicates for Sper01 to reveal the diet, and a single PCR for Mamm02 to identify the mammalian species. All experiments included several extraction controls (no template at DNA extraction step), blanks (no primer, no template), PCR negative controls (water) and PCR positive controls (mammals: *Ursus arctos*, plants: *Stephanotis floribunda*). As additional controls, we also included DNA extracts from dung samples of known ungulate species from zoos or collected by hunters from harvested animals.

Table 2. *Summary of primers used in the DNA metabarcoding experiments*

| Taxon | DNA type/ region | Primer name | Forward/ reverse/ blocking primer | Primer sequence 5'-3' |
|---|---|---|---|---|
| Plants | Chloroplast | Sper01[a] | Forward | GGGCAATCCTGAGCCAA |
| | (trnL UAA) | | Reverse | CCATTGAGTCTCTGCACCTATC |
| Mammals | Mitochondrial | Mamm02[b] | Forward | CGAGAAGACCCTRTGGAGCT |
| | (16s rDNA) | | Reverse | CCGAGGTCRCCCCAACC |
| | | P007_Blk_ Homo | Human blocking | ccaaccGAAATTTTTAATGCAGGTTT GGTAGTT-C3 |

a) Taberlet et al. (2018)
b) Giguet-Covex et al. (2014), Taberlet et al. (2018)

### 2.4.3 DNA purification, pooling of PCR products and sequencing

PCR products were purified using the MinElute PCR purification kit, checked via capillary electrophoresis (QIAxel; QIAgen GmbH), and pooled in equivolume mixes before sequencing. Sequencing libraries were prepared

according to the MetaFast protocol (www.fasteris.com/metafast) and sequenced on an Illumina HiSeq 2500 platform using a paired-end approach (2 x 125 bp).

### 2.4.4 Analysis, filtering and taxonomic annotation of sequences

For the initial processing of the sequencing data we used the OBITools software (http://metabarcoding.org/obitools). We used *illuminapairend* to align and merge the forward and reverse reads of the same DNA fragments into a consensus sequence. Sequences with low alignment scores (< 40) were discarded. We then used *ngsfilter* to identify primers and tags and to assign reads to samples. Identical sequences were dereplicated with *obiuniq*, while retaining the information from which sample they originated. For further processing of the data, we stored them in a relational database using PostgreSQL (https://www.postgresql.org) and used R (R Core Team, 2017). We populated the database with marker-specific local reference libraries for taxonomic annotation of our mammalian (see Spitzer *et al.* (2019)) and plant sequences. For the latter we merged an already existing library of sequences for arcto-boreal vascular plants (Sønstebø *et al.*, 2010; Willerslev *et al.*, 2014) and bryophytes (Soininen *et al.*, 2015) with further species sequences based on local plant inventories (Heinken, 2019) as well as agricultural crops (European Commission) by extracting them from the EMBL (European Molecular Biology Laboratory) nucleotide database (Silvester *et al.*, 2018). Taxonomic relationships were extracted from the NCBI (National Center for Biotechnology Information) taxonomy database (Sayers *et al.*, 2009). We then carried-out a further filtering of the data by removing singleton sequences and ambiguous sequences containing 'N' (IUPAC code). For mammalian sequences, we also removed sequences > 100bp, i.e., those beyond the length of DNA fragments typically amplified by the Mamm02 primer. We compared the relative frequency of MOTUs (molecular operational taxonomic units), which corresponded exactly to a sequence in our mammalian reference library to the distribution of MOTUs not corresponding to a reference sequence and removed all sequences representing < 1% in a PCR. We also removed sequences of < 40bp which mostly corresponded to bacterial artefacts and PCRs with < 500 reads, indicating poor amplification success. Mammalian species was assigned according to the most abundant sequence in the sample which also matched exactly with a sequence from the reference library. If we detected more than one species in a sample, we only kept samples in which the first annotated sequence (i.e., the assigned species) was at least twice as abundant as the second most abundant sequence. For the plant sequences, we only kept reads with a length of at least 5bp. For each DNA extract, we had three PCR replicates. We only kept MOTUs

which represented at least 1% in at least 3 PCR. To assess consistency across replicates, we calculated the distances of PCR replicates from their barycentres based on their sequence composition (PCR distances) and the distances between barycentres (sample distances). In consistent PCR reactions, PCR distances should be small (= zero under hypothetical perfect conditions with identical amplification across PCR replicates) compared to sample distances. We log-transformed sample distances to attain an approximately normal distribution and used the distance corresponding to the 5% percentile as a quality threshold for PCR replicates. We then removed all outlier PCR replicates with a distance larger than this threshold. In a graph-partitioning approach, we plotted PCR and controls and removed PCR clustering with controls as potentially contaminated or with poor amplification success (< 1000 reads). For the remaining two or three PCR replicates per sample, we averaged the reads per MOTU. We considered MOTUs with low similarity (< 80% identity) to their closest match in the reference database as likely to be PCR/sequencing errors, chimeras or highly degraded sequences and excluded them from further analyses.

### 2.4.5 Quantification of diet composition (Papers III & IV)

To confer the same weight to each faecal sample, we converted read abundances into relative read abundances (RRA), representing the proportion of each MOTU in each faecal sample. In addition to the standard filtering described earlier we also removed MOTUs that did not represent at least 2.5% in at least one sample from the final datasets for Paper III and IV (Bison *et al.*, 2015). RRA has frequently been used as a quantitative measure for the proportional composition of diets (Bison *et al.*, 2015; Craine *et al.*, 2015; Kartzinel *et al.*, 2015; Deagle *et al.*, 2019; Kowalczyk *et al.*, 2019; Pansu *et al.*, 2019), yielding similar conclusions to those derived from presence/absence data (Willerslev *et al.*, 2014; Kartzinel *et al.*, 2015; Kowalczyk *et al.*, 2019). I therefore decided to use RRA to characterize molecular diet data throughout this thesis. An alternative method for quantification, the frequency of occurrence (FOO), is discussed in section 3.5 and FOO results for my data are included as Appendix 2c.

## 2.5 Statistical analyses

Unless otherwise stated, all analyses in this thesis were carried-out in R (R Core Team, 2017) at a significance level of $\alpha = 0.05$ for statistical tests. For an initial assessment of the distribution of response variables in models, I generally used Cullen-and-Frey graphs provided in the R-package *fitdistrplus* (Delignette-Muller & Dutang, 2015).

### 2.5.1 Indices of diversity, niche overlap, and selectivity (Papers I, III and IV)

The most basic measure of diet diversity is arguably the number of different food items (i.e., MOTUs) that are detected in a faecal sample. This is also referred to as richness (*S*) or alpha diversity. I considered a MOTU as detected when its read count after the filtering steps was greater than zero in a sample. One disadvantage of using simple richness is that rare diet items receive equal weights as common ones.

A more balanced measure for diet diversity is provided by the Shannon-Wiener diversity index (*H'*) also known as the Shannon entropy:

$$H' = -\sum p_i \ln(p_i)$$

where $p_i$ is the relative abundance ($n_i/N$) of species *i* (Pielou, 1975). The Shannon-Wiener index accounts for both richness and evenness in the diet; a value of zero corresponds to a diet containing only a single item. The index has frequently been used to describe dietary niche width (Mysterud, 2000; Bolnick *et al.*, 2007; Redjadj *et al.*, 2014; Bison *et al.*, 2015; Pansu *et al.*, 2019). One disadvantage lies in that the index has a nearly flat slope when diversity is high, making the interpretation of differences in diversity difficult (Jost, 2006). I therefore followed suggestions by Jost (2006) and converted the Shannon entropy to Hill-numbers (Hill, 1973) for q = 1 ($^1D_\alpha$) or 'true diversity' (Jost, 2006). It is computed as the exponential of the Shannon entropy (Jost, 2006; Kowalczyk *et al.*, 2019). Dietary niche width (Paper III) thus corresponds to:

$$DNW = \exp(H')$$

Habitat diversity in Paper III was defined in the same manner. The Shannon entropy was calculated using the R-package *vegan* (Oksanen *et al.*, 2017).

In Paper III, I also quantified among-individual dietary variation (*V*) for each deer species and season using R-package *RInSp* (Zaccarelli *et al.*, 2013) as described in Pansu *et al.* (2019). This approach uses a modification of Schoener's (1968) proportional similarity index ($PS_i$). This index represents the overlap of an individual diet with the population diet. The population-wide measure of among-individual dietary variation can then be calculated as (Bison *et al.*, 2015):

$$V = 1 - \overline{PS_i}$$

Values of $V = 0$ indicate that individuals utilize the same range of resources whereas values approaching 1 correspond to higher among-individual variation (Bolnick *et al.* 2007).

For calculating dietary niche overlap (Papers I & III), I used the index of Pianka (1988). This index has been used by several authors to characterize overlap between diets (e.g., Azorit *et al.* (2012), Putman (1996), Lovari *et al.* (2014), Pansu *et al.* (2019)). It can be used to describe both intraspecific and interspecific overlap and assumes values between zero (total dietary niche separation) to one (complete overlap, i.e., identical diets). The index is defined as:

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{[(\sum p_{ij}^2)(\sum p_{ik}^2)]^{1/2}}$$

where $p_{ij}$ and $p_{ik}$ are the proportion corresponding to the $i$th partition of a given resource to the total resource use by species $j$ and $k$ (Putman, 1996). Pianka's index was calculated with R-packages *spaa* (Zhang, 2016) and *EcoSimR* (Gotelli *et al.*, 2015).

To determine selectivity for a number of important food items that formed large proportions of diets and/or corresponded to commercially valuable tree species such as spruce and pine (Paper III), I used Jacobs' (1974) index which relates the utilization of food items (i.e., their proportion in the diet) to their relative availability in the environment. The index ranges from -1 to 1, with negative values indicating utilization below availability (avoidance) and positive values corresponding to utilization above availability (preference). A value of zero means that a food item is utilized in proportion to its availability. Jacobs' $D$ is calculated as:

$$D = \frac{r - p}{r + p - 2rp}$$

where $r$ represents the proportion of a food item in the diet and $p$ the accessible proportion of the same food item in the environment (i.e., its relative availability).

### 2.5.2 Diet and resource partitioning at the European scale (Paper I)

To assess the applicability of Hofmann's feeding types, I first measured the location of ruminant species along the grass-to-browse continuum in Hofmann's (1989) graph (Supporting Information S2 in Paper I). Onto this template, I then plotted the diets of the four deer species (moose, roe deer, red deer, and fallow deer) extracted from the European literature and used density isopleths to illustrate their plasticity (i.e., variations in browse and grass contents of their diets) (Figure 3).

To investigate finer-scale partitioning of food resources between species, I used equilateral mixture triangles (EMT, Raubenheimer (2011)) and non-metric

dimensional scaling (NMDS) as provided in the R-package *vegan* (Oksanen *et al.*, 2017).

Intra-and interspecific dietary overlap was calculated as Pianka's index as described in the previous section. The analyses of interspecific dietary overlap were largely restricted to roe deer and red deer because they were the only two species for which diet data was available for all seasons and European regions. Following suggestions by Mysterud (2000), I also calculated Pearson's correlation ($r_p$) between dietary overlap and distance in feeding type for winter and the growing season (i.e., spring-autumn).

To test whether diet compositions within each ungulate species differed across habitat types and season, I used G-tests of independence (MacDonald, 2014) followed by Holm-corrected pairwise post-hoc comparisons.

### 2.5.3 Dung morphometry (Paper II)

The morphometric measurements did not meet the assumptions of standard ANOVA such normality of residual errors. To test for interspecific differences, I therefore used non-parametric Kruskal-Wallis tests followed by Dunn's post-hoc test with Benjamin-Hochberg corrections. I also used discriminant analysis with jacknifed cross-validation (R-package *MASS* (Venables & Ripley, 2002)) on the morphometric variables (log10-transformed) to assign pellets to species.

To test the effect of observer experience on species identification success (true/false, based on Field ID vs. DNA ID), I used a logistic regression with 'species', 'experience', and their interaction as predictors. Post-hoc pairwise comparisons were carried-out using R-package *lsmeans* (Lenth, 2016).

### 2.5.4 Diet and resource partitioning in Sweden (Papers III & IV)

In my analyses, response variables frequently corresponded to proportions, i.e., assumed values in the standard unit interval (0,1). These included dietary overlap (Pianka's index, Paper III) or the proportions of particular food items in ungulate diets such as pine or *Vaccinium* spp. (Paper IV). I therefore applied beta-regression models to these data as suggested by Ferrari and Cribari-Neto (2004) using the R-package *betareg* (Cribari-Neto & Zeileis, 2010). In Paper III, I tested the effect of season, habitat diversity, proportion of arable land, and ungulate density on interspecific dietary overlap. In Paper IV, I used a beta regression to test the effect of deer density, food availability, and snow depth on the consumption on pine and *Vaccinium* spp. by moose. I also used a beta regression in combination with Tukey-adjusted post-hoc tests from R-package *emmeans* (Lenth, 2019) to test for differences in pine and *Vaccinium* spp. utilization by all

four deer species along a gradient in deer density. To test for differences in habitat composition along the same density gradient, I used a Chi-square test for equality of proportions.

To test the effect of season, habitat diversity, the proportion of arable land, and ungulate density on DNW (Paper III), I used generalized linear models (GLM) with Gamma distribution and a log-link function.

To visualize of feeding niches, their overlap and association with major food items, I used NMDS ordinations (R-package *vegan* (Oksanen *et al.*, 2017)).

# 3 Results and discussion

## 3.1 Ungulate diets across Europe (Paper I)

The literature search yielded 265 diet profiles contained in 87 publications spanning 17 European countries. Only 7% of these studies investigated trophic interactions between more than two ungulate species and the majority (71%) focussed on the diet use of only a single species.

On average, the reported diet compositions for the four deer species fit well with the predictions of Hofmann's classification of feeding types but I also found large intraspecific variation, especially for the mixed feeders (red and fallow deer) (Figure 3). As expected, the NMDS ordination showed partitioning along the axis of woody browse to concentrates (forbs, fruits, and seeds) for browsers (moose and roe deer), whereas red and fallow deer separated more along the axis from woody browse to grass (Supporting Information S3 in Paper I). During winter, all ungulate species (including wild boar) switched to higher proportions of woody browse in their diets (Figure 4). Diet compositions at the intraspecific level differed between most habitat types but proportions of major food items linked to feeding type (e.g., grasses for mixed feeder and dicots for browsers) remained relatively constant across habitat types (Figure 3 in Paper I).

Intraspecific dietary overlap was highest for moose and lowest for the omnivorous wild boar. In northern and central Europe intraspecific dietary overlap between roe deer and red deer showed a U-shaped annual pattern (high during spring and winter, lower during summer and autumn). In southern Europe, dietary overlap remained relatively constant across the seasons (Figure 4 in Paper I). During both the growing season and winter, dietary overlap was negatively correlated with distance in feeding type ($r_p = -0.45$, $P < 0.001$ and $r_p = -0.46$, $P < 0.001$ respectively), i.e., the more ungulates differed in feeding type, the less their feeding niches overlapped.

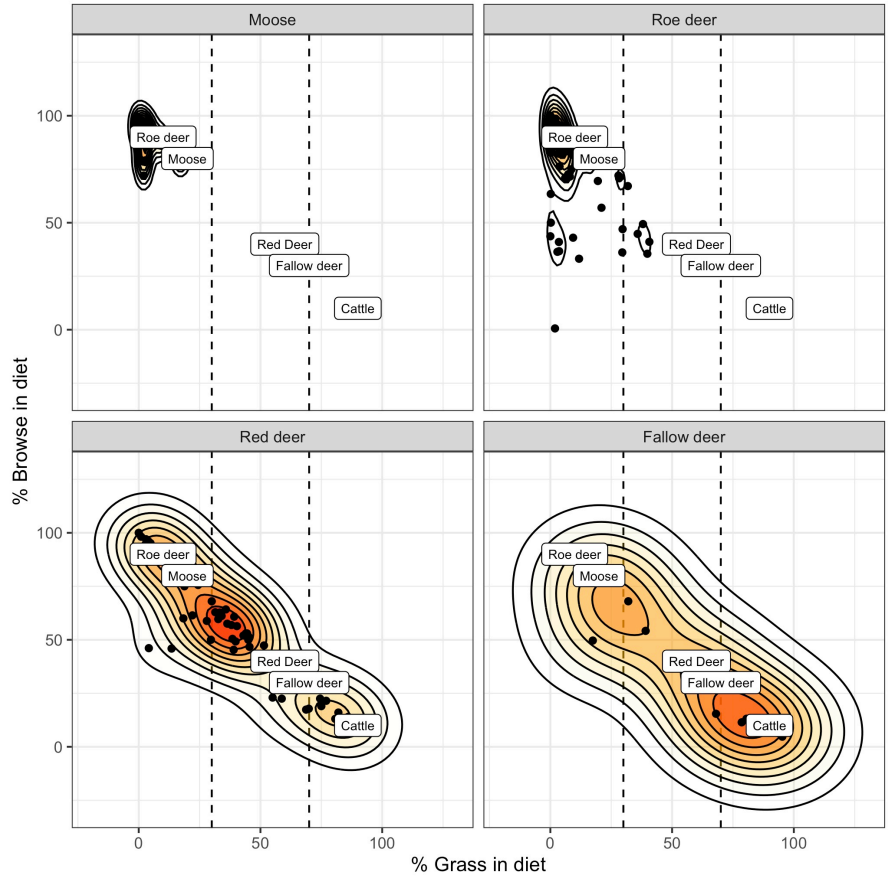


*Figure 3.* Proportions of browse and grass reported in the European literature in the context of Hofmann's (1989) classification of feeding types. The dashed lines correspond to the thresholds between browsers, mixed feeders, and grazers (from left to right). The boxed species names within plots indicate their placement within Hofmann's graph. Each dot represents a diet profile during the growing season for the species indicated in the facet title. For example, the bottom-left plot displays red deer diets from across Europe. Most red deer diets cluster close to the position suggested for red deer whereas others resemble cattle or moose diets. Density isopleths and colours illustrate the data distribution with darker tones representing higher density, i.e., the most characteristic fraction of the data. (from Paper I)

As was predicted by Hofmann's feeding types, the data showed that mixed feeders can perform seasonal switches between browse and grass and/or adopt the feeding type most suited to local conditions. Browsers appear more restricted and might even be obligatory non-grazers as was suggested by Van Wieren (1996). This has some interesting implications for multi-species communities containing both feeding types. An increase of mixed feeders in such communities would probably be more detrimental to browsers than vice versa.

During winter, mixed feeders would add to the browsing pressure on woody vegetation, thereby contributing to the depletion of browse forage in the landscape. During the vegetation period, mixed feeders would be better adapted to compensate for a shortage of browse by increasing their intake of grass. Browsers do not appear to have this option. Under conditions of food limitation, the relationship between mixed feeders and browsers might become amensalistic with the former potentially replacing the latter. This process could be exacerbated in anthropogenic landscapes where managers may be inclined to counteract the increasing browsing impact by reducing the number of browsers, thereby adding to the competitive pressure.

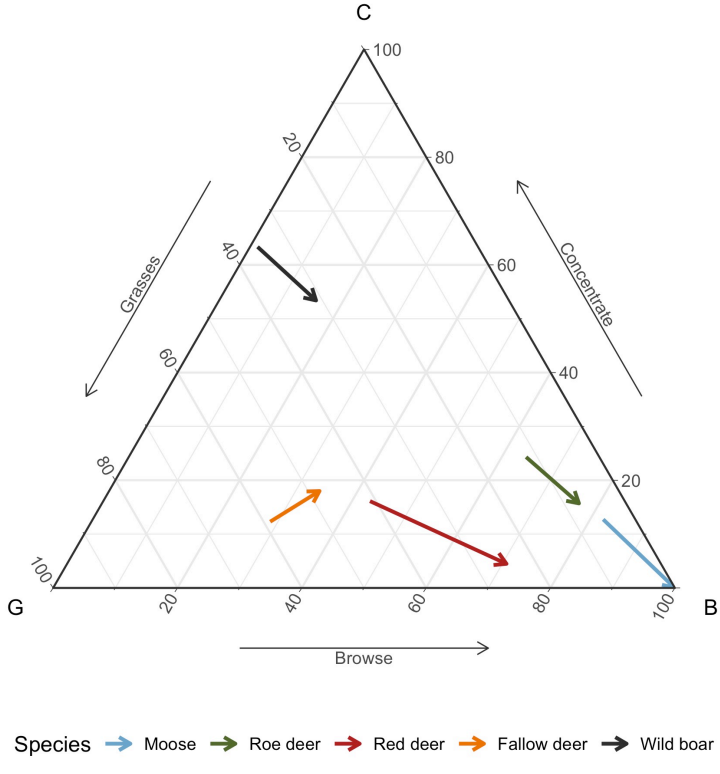


*Figure 4.* Separation of ungulate diets in the dimensions of woody browse (B), grass (G), and concentrates (forbs, fruits, and seeds; C). The arrows show the changes in average diet composition from the growing season (blunt end) to winter (arrow heads). (from Paper I)

## 3.2 Species misidentification (Paper II)

In total, 87% (3889 samples) of the collected faecal samples from nine ungulate species passed the DNA metabarcoding filtering steps. Across the European data set, average species misidentification rates ranged from 0.6% for horse (*Equus ferus*) to 41.1% for roe deer. For deer species in Sweden, misidentification of faecal pellets was lowest for moose (4.6%) and highest for fallow deer (39.3%). For further details, see Table 1 in Paper II. Most identification errors occurred between species of similar size and the same taxonomic family; for example, between roe deer, red deer and fallow deer or between European bison and cattle (Figure 5).

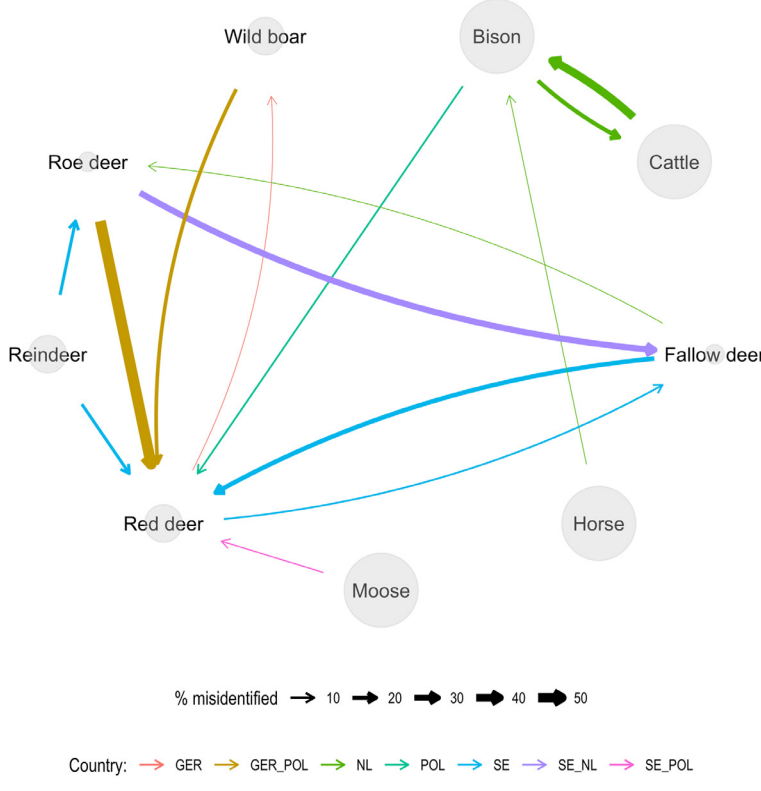


*Figure 5.* Overview of the most common identification mistakes of ungulate dung pellets. The species names correspond to the Field ID and the arrows point to the correct species as identified by DNA testing. The size of the grey circles denotes body mass. Arrow thickness indicates the proportion of misidentification and the colours denote study sites: GER-Germany, NL-Netherlands, POL-Poland, and SE-Sweden. (from Paper II)

From the subset of samples that were measured as part of the dung morphometry experiment in Sweden, 78% (196) passed the filtering steps. Reindeer yielded

only three viable samples and was thus excluded from the analyses. Species had a significant effect on all morphometric measurements (Kruskal-Wallis tests, $P < 0.05$) but due to large overlap in measurements, dung morphometry only clearly distinguished moose but not roe deer, red deer, and fallow deer (Figure 6).

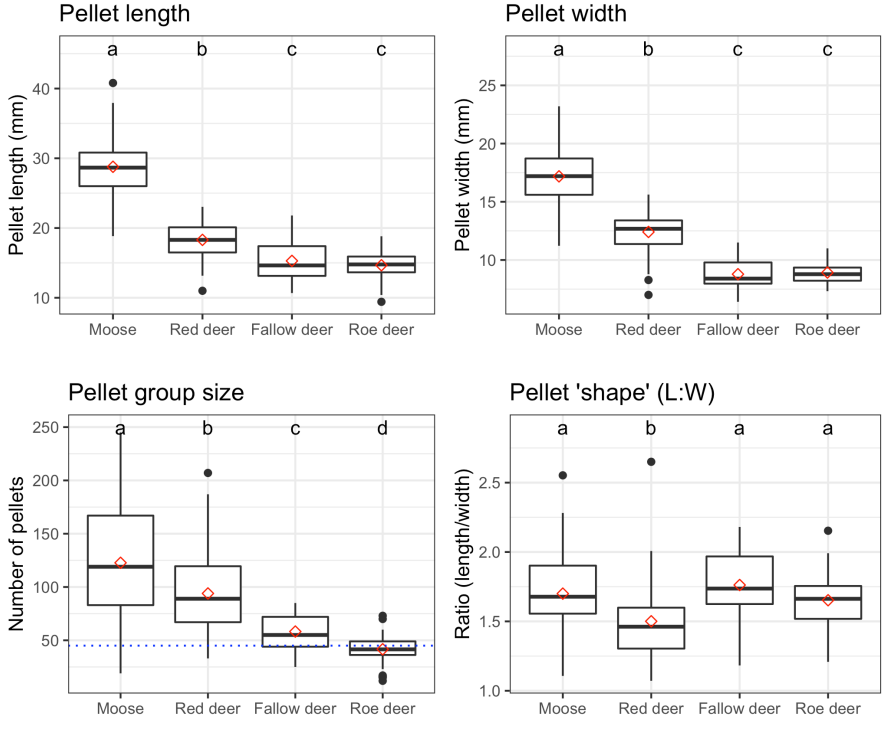


*Figure 6.* Comparisons of morphometric measurements on faecal pellets from four deer species in Sweden. Mean values are denoted by red diamonds and different letters indicate significant differences. The dotted line in blue indicates a commonly used threshold (N = 45) for discriminating between roe and fallow deer. (from Paper II)

For the latter two species, experienced observers performed better than novices but still misidentified a large proportion (26 % and 17% respectively). Discriminant analysis based on the morphometric measurements performed better than observers only for fallow deer pellets ($\chi^2 = 6.48$, df = 1, $P = 0.01$) but still assigned only 60% of samples correctly. During winter and spring overall identification success (averaged across all four deer species) was higher than during summer and autumn.

These results highlight the difficulty in using pellet group counts for monitoring ungulate abundance in communities with species of similar size.

Such counts, however, can remain useful as an overall density index or when the monitoring is aimed at species with clearly different dung morphologies, such as moose. For example, in the study on possible trophic competition between moose and smaller deer (Paper IV), I could still exclude moose pellet group counts with high confidence from the deer density index comprised of the three smaller species.

## 3.3 Trophic resource use and partitioning (Paper III)

In total, 2558 (77%) of faecal samples from the four deer species passed the DNA filtering steps (Table 2 in Paper III). I detected 207 MOTUs in the overall diet data (Appendix 2a) but an individual faecal sample typically contained only 20 – 40 MOTUs. This diet richness (S) was highest for fallow deer and lowest for moose (Table 2 in Paper III). A comparison of average annual diets for each deer species at the taxonomic resolution of family or higher (78 categories) showed that deer diets in the study area were dominated by comparatively few of these categories. Proportions of DNA reads (RRA) were high for Ericaceae (represented largely by ericaceous shrubs of the genera *Vaccinium*, *Calluna*, and *Empetrum*), Pinaceae, Betulaceae, Rosaceae, Fabaceae, Poaceae, and Salicaceae (Figure 7).

The monthly diet profiles at the resolution of 10 major food categories showed high utilization of *Vaccinium* spp. by all four deer species throughout the year, and particularly during winter and spring when RRA of *Vaccinium* spp. in the diet frequently represented 50% or more (Figure 8). During summer and autumn, the proportion of *Vaccinium* spp. in moose diet remained higher than for the smaller deer species. During winter and spring, moose diet was dominated by pine and also contained small amounts of juniper (*Juniperus* sp.). All deer species consumed small amounts of spruce (usually < 5% of diets) with the highest proportions being utilized by red deer (12%) and fallow deer (17%) during late spring. Forbs and graminoids comprised large proportions in the diets of the smaller deer (30-60% during the summer) but were less prominent in moose diets (5-15%). The proportions of graminoids in the diets of the mixed feeders (red deer and fallow deer) were lower than expected (typically < 15% of DNA reads). The relative comparison of graminoid utilization across deer species, however, corresponded well with the ranking according to Hofmann's feeding types, i.e., values were lowest for moose and highest for fallow deer. The exception were roe deer diets which contained graminoids in similar proportions to those of red and fallow deer rather than moose (Figure 2c in Paper III).

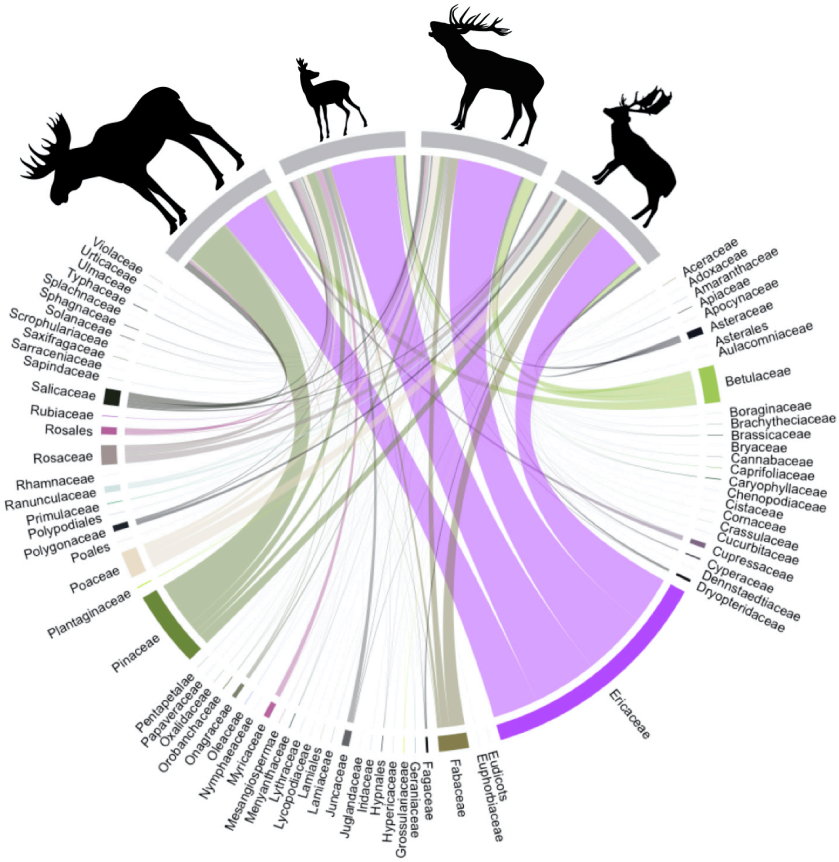


*Figure 7.* Average annual diet composition as determined by DNA metabarcoding for moose, roe deer, red deer, and fallow deer (left to right) in Sweden. Diet data have been aggregated at the taxonomic resolution of plant family or higher. (from Paper III)

Forbs were generally utilized at higher proportions than suggested by their relative availability in the landscape (Jacobs' D > 0, Figure 9), whereas graminoids were typically consumed less or approximately equal to availability. Broadleaf forage was eaten below availability in winter but above or near availability during the other seasons by all deer species. Among the coniferous trees, spruce was consumed below availability by all deer species in all seasons. Pine was always utilized above availability by moose and frequently also consumed near availability by the smaller deer.

The seasonal pattern of intraspecific dietary variation *V* was similar for all deer species (low during spring and winter and higher during summer and

autumn). During all seasons, values of $V$ were lower for moose than for the smaller deer species (Figure 4b in Paper III).

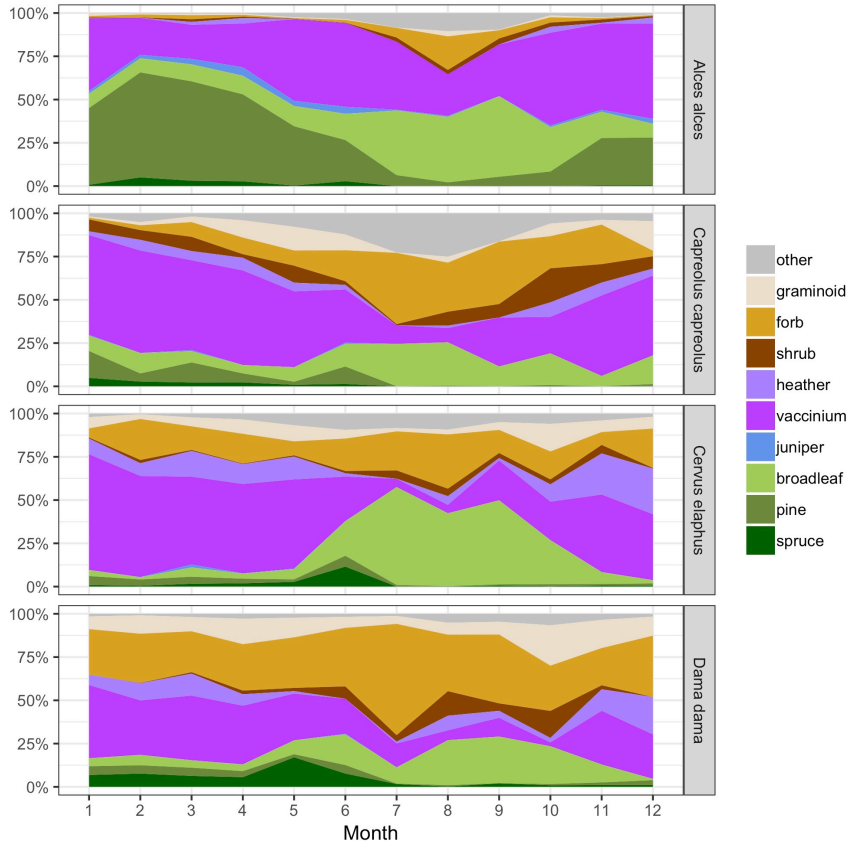


*Figure 8.* Average monthly diet composition of four deer species in Sweden at the resolution of 10 food categories. The percentages on the y-axis correspond to RRA. (from Paper III)

DNW was lowest for moose and highest for fallow deer but varied only little across seasons (Figure 4a in Paper III). I found no significant interactions between season and the other predictors (habitat diversity, the proportion of arable land, and ungulate density) on DNW. Increasing proportions of arable land led to significant increases in DNW for moose, red deer and fallow deer. I found no significant effects of habitat diversity and ungulate density on DNW.

Using the same predictor variables as for DNW, I found no significant effects on dietary overlap between the species pairs of moose-roe deer and red deer-fallow deer. For moose-red deer, an increase in the proportion of arable land significantly reduced dietary overlap in summer. Dietary overlap between moose

and fallow deer decreased with both higher ungulate density and proportion of arable land, but during spring and summer increased with greater habitat diversity. Dietary overlap between roe deer and red deer decreased with habitat diversity and increased with arable land. For roe deer and fallow deer, dietary overlap was only affected by season, i.e., increased during both spring and winter compared to autumn (see Table 4 from Paper III).

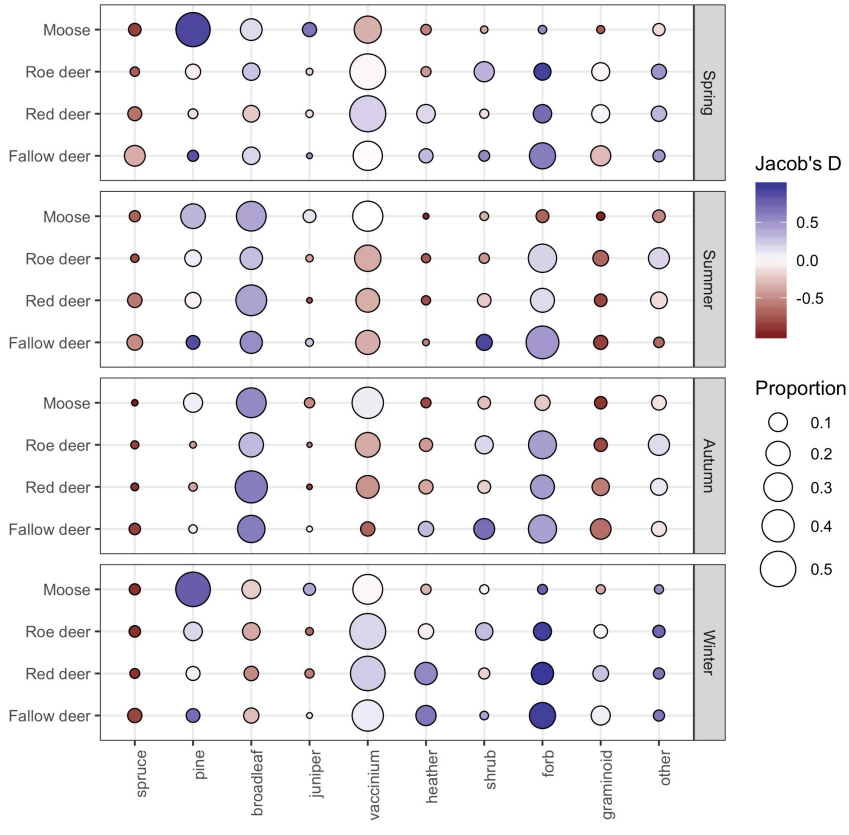


*Figure 9.* Selectivity (Jacobs' D) of 10 major food items by four deer species across the seasons in Sweden. Blue colours indicate utilization above relative availability ('preference') and red colours utilization below relative availability ('avoidance'). Circle size corresponds to proportion in the diet (as RRA), i.e., rows sum up to 100%. (from Paper III)

The comparisons between intraspecific and interspecific dietary overlap showed higher intraspecific dietary overlap for moose during all seasons (Figure 10). For the smaller deer species, I detected no clear separation between intra- and interspecific dietary overlap. Intra- and interspecific dietary overlap was

typically higher during winter and spring than during summer and autumn. An exception to this was the dietary overlap between moose and red deer that was highest during autumn.

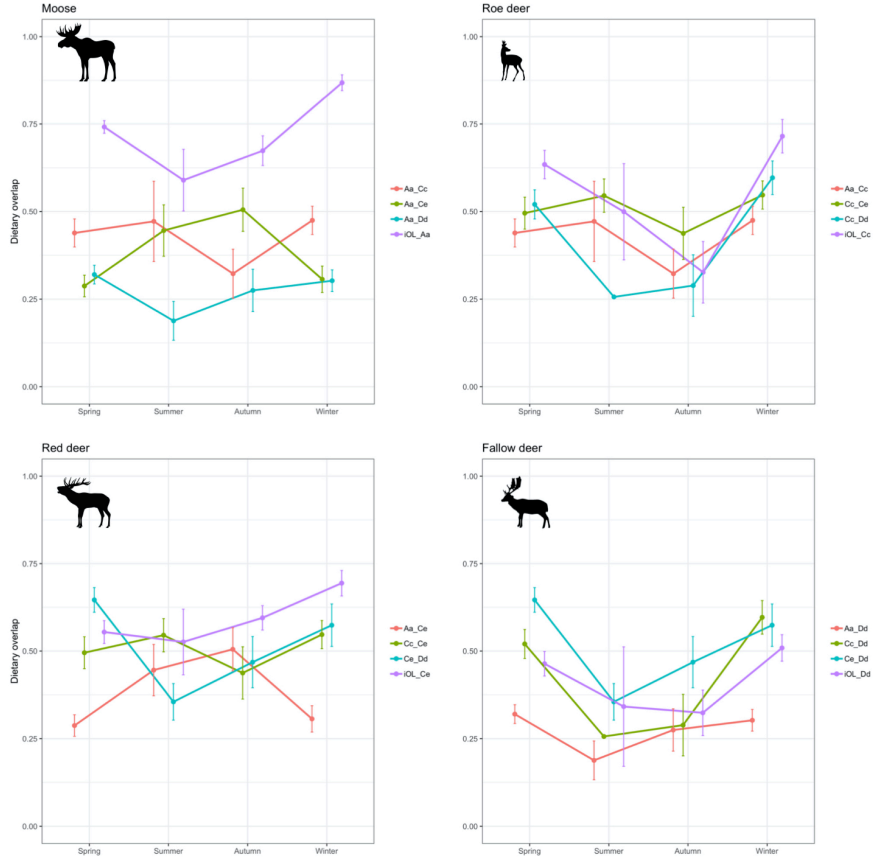


*Figure 10.* Comparison between intra- and interspecific dietary overlap (Pianka's index) during different seasons. The error bars show the standard error. Each facet displays the intraspecific dietary overlap (iOL, purple) of the respective deer species and the interspecific dietary overlap with the other three deer species (indicated by the colours red, green, and blue). Species abbreviations in the legends correspond to: Aa = *Alces alces* (moose), Cc = *Capreolus capreolus* (roe deer), Ce = *Cervus elaphus* (red deer), and Dd = *Dama dama* (fallow deer). (from Paper III)

Generally, the NMDS ordinations showed a generally large overlap of the dietary niches of all four deer species. Their niches never fully separated but the strongest partitioning occurred over pine and juniper which was almost exclusively utilized by moose, especially during spring and autumn (Appendix 1b).

The results support the view of dietary plasticity among the four deer species, especially for the mixed feeders, red deer and fallow deer. The high utilization of woody browse highlights their adaptability to forest-rich northern environments. Ericaceous shrubs appear to be an important food source for all four deer species and the role of these small shrubs as a possible driver of resource partitioning among the four deer species warrants further investigation. Of interest is also the high dietary overlap between moose and red deer during the vegetation season. Additional research is needed to clarify if this stems from the utilization of broadleaves as I suggested and whether it might drive moose to increasingly switch to other food items such as pine. The relatively large proportions of forbs and graminoids in the diet of the smaller deer species during winter may indicate supplementary feeding and could have affected the results for DNW and dietary overlap. Further research should address this question. For moose, intraspecific dietary overlap was higher than interspecific overlap with any of the smaller deer species. This suggests that for moose in our study area the potential for competition might currently be higher with conspecifics rather than with other deer species.

## 3.4 Trophic resource competition (Paper IV)

A total of 2629 (79 %) faecal samples passed the DNA quality filtering criteria. Habitat composition did not differ among transects of different deer density classes ($\chi^2 = 23.92$, $P = 0.33$). Mean deer density was 22.3 pellet groups/1000m$^2$. Snow depth on transects ranged from 0 - 38.5 cm ($\bar{x} = 6.9$ cm). *Vaccinium* spp. represented the most abundantly available forage item (Supporting Information S3a in Paper IV). Pine availability was lowest on transects with high deer density (Supporting Information S3b in Paper IV).

Pine and *Vaccinium* spp. dominated moose diets (> 75%) during both winter and spring (Figure 1d in Paper IV). In winter diets of moose, the proportion of pine significantly increased with increasing deer density whereas the proportion of *Vaccinium* spp. declined (Table 1 in Paper IV). Increasing snow depth also led to higher consumption of pine but did not affect the use of *Vaccinium* spp. Spring diets largely corroborated the findings for winter. On transects with high deer density, moose consumed significantly more pine and less *Vaccinium* spp. (Figure 11). The proportion of pine in the diets of the three smaller deer species did not significantly differ between density classes. The consumption of *Vaccinium* spp. by red and fallow deer was unaffected by deer density whereas roe deer consumed more *Vaccinium* spp. in areas with high deer density.

Throughout the year, the proportion of pine in the diets of the three smaller deer species was low (typically < 10%). For moose, pine consumption peaked

during late winter (> 50%) and then declined from spring to a low in August before increasing again. This overall pattern of pine consumption by moose was observed for all deer density classes. However, in areas of high deer density the proportions of pine in moose diet were generally higher. The utilization of *Vaccinium* spp. followed an annual pattern that was similar for the three smaller deer species, but different for moose. *Vaccinium* spp. consumption by red, roe and fallow deer resembled a sine curve with a maximum of 50-60% around March-April and a minimum of approximately 10-20% around August. Moose showed less seasonal variation, particularly on transects with low and medium deer densities. In areas of high deer density, the proportions of *Vaccinium* spp. in moose diet were generally lower but peaked in August when consumption by the smaller deer species was lowest (Figure 3 in Paper IV).

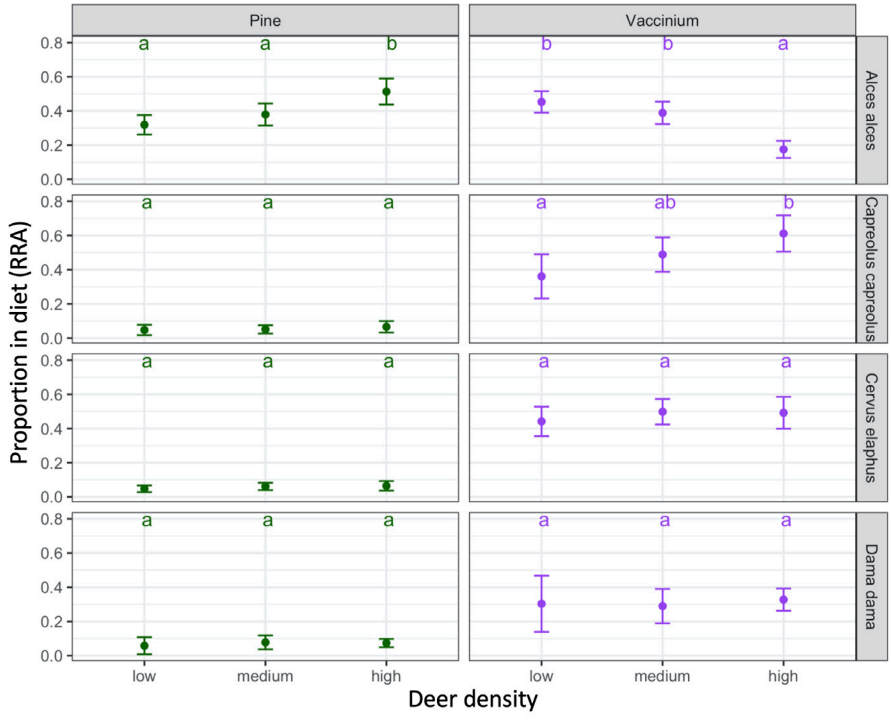


*Figure 11.* Utilization of pine (green) and *Vaccinium* spp. (purple) by four deer species at three deer density classes. The error bars represent 95% confidence intervals. Different letters within facets indicate significant differences. (from Paper IV)

These findings suggest that feeding competition with smaller deer species in the field layer may drive moose to switch to food items in higher foraging strata that also offer larger bites such as pine. Managing the food supply in the field layer,

particularly *Vaccinium* spp., and controlling the populations of smaller deer may help to mitigate the forestry-moose conflict over browsing pressure on pine.

## 3.5 DNA metabarcoding

On average, approximately 80% of the faecal samples amplified and passed all the subsequent filtering steps of the DNA metabarcoding process. This number is conservative as we only included samples that passed both species and diet identification. Additionally, I removed instances of suspected contamination such as from hare (*Lepus* sp., see Paper II), which affected ~ 2% of the samples. For plant sequences, on average only ~1% of the reads retained per sample (following all filtering steps, and prior to taxonomic annotation) could not be matched to a sequence in the reference library. The final diet data set for the deer species in Sweden contained 207 MOTUs (Appendix 2a).

In the context of DNA metabarcoding, a MOTU corresponds to a set of sequence variants merged into a single unit based on a given similarity threshold. As a result, MOTUs can be taxonomically vague and correspond to a group of sequences, a species, genus or higher taxonomic order (Taberlet *et al.*, 2018). In my dataset, 46% of the plant MOTUs were assigned at species level, 34% at genus, 15% at family (including subfamily, tribe and subtribe) and 5% at the rank of order or clade. For some analyses I aggregated MOTUs further, e.g., at family level (Figure 7) or into major functional food groups like *Vaccinium* spp. which contained all *Vaccinium* MOTUs from genus to species level (see Appendix 2a). Marker limitations are also important to consider in DNA metabarcoding studies. The Sper01 primer I used only amplifies chloroplast DNA which means that I could not detect fungi, lichen or animal matter in the diet. This restriction is one of the reasons why omnivorous wild boar (Paper I) and reindeer, which feed extensively on lichen (Ophof *et al.*, 2013), were not included in the diet analyses.

Further, the taxonomic resolution of the P6 loop of the trnL intron of chloroplasts varies between plant taxa, limiting the discriminatory power of the barcode (Taberlet *et al.*, 2007). For example, it is quite limited for Poaceae or Rosaceae which prevented quantification of several individual species within these families; e.g., rowan (*Sorbus aucuparia*, Rosaceae) that is highly favoured by moose (Månsson *et al.*, 2007). For my analyses this presented no major obstacle as these two families comprised rather small proportions of the overall diets (see Figure 7) and I was primarily interested in partitioning along major food categories. If a finer taxonomic resolution is needed, additional barcodes and multiplex reactions can be used (De Barba *et al.*, 2014) but this carries higher costs and requires substantially more time. Using relative read abundance (RRA)

as a quantitative measure for diet composition is becoming increasingly more common among researchers (see section 2.4.5), but also has limitations. Plant taxa and tissues might have varying concentrations of chlorophyll and different digestibility which could affect the amount and quality of DNA of the respective plant taxa in a faecal sample. Amplification bias during PCR (Pawluczyk *et al.*, 2015; Nichols *et al.*, 2018) can also affect the quantities of sequence reads and result in over- or underestimations of diet components. The alternative approach of quantifying DNA metabarcoding data purely based on the presence/absence of MOTU or their frequency of occurrence (FOO) across samples is prone to exaggerate the importance rare items (Pansu *et al.*, 2019). For example, a MOTU representing 0.5% of reads in a sample would be just as 'detected' as one representing 50%. In the worst case, too much weight could be conferred to spurious MOTUs (e.g., low-level contaminants) remaining in the data even after the most conservative filtering (Taberlet *et al.*, 2018). Moreover, large sample sizes are needed for FOO to be informative. RRA has frequently been shown to yield similar results to other quantification methods, e.g., isotopic proportions (Kartzinel *et al.*, 2015), microhistology (Nichols *et al.*, 2016), and presence/absence (Pansu *et al.*, 2019). A good agreement between FOO and RRA for herbivore diets has also been reported by Taberlet *et al.* (2018). For my own data, this relationship is illustrated in Figure 12 which also highlights the effect of different detection thresholds for the presence/absence of MOTUs.

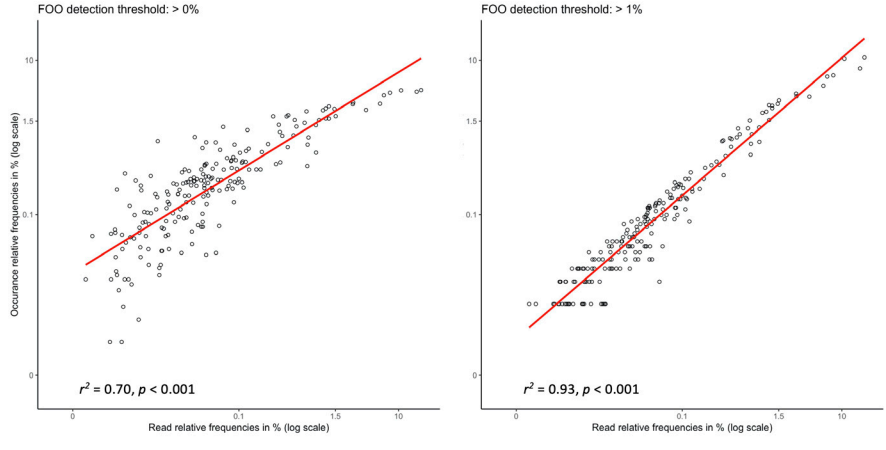


*Figure 12.* Comparison between read relative abundance (RRA, x-axis) and occurrence relative frequency (y-axis) as quantification methods for DNA metabarcoding data. Each circle represents one MOTU in the average diet of four deer species. Detection thresholds of MOTUs for frequency of occurrence (FOO) counts were set to > 0 (left) and > 1% (right).

A more conservative detection threshold (e.g., > 1%) reduces the possible overvaluation of rare MOTUs in FOO data and leads to greater agreement with RRA quantification (r = 0.93). Increasing detection thresholds could, however, also heighten the risk of removing MOTU from the data that truly are rare in the diet, e.g., occurring only in a small part of the study area or are eaten only under very specific circumstances. These questions need to be considered by researchers on a case-by-case basis depending on the objectives of their study and ancillary knowledge about the study system.

# 4 General discussion

The results presented in this thesis suggest that thirty years after its inception, Hofmann's (1989) ruminant diversification hypothesis of different feeding types continues to be a useful starting point for the investigation of trophic resource use and partitioning in multispecies ungulate communities. A key aspect that emerged from the European literature as well as my own data from Swedish ungulate communities, however, is the apparent dietary plasticity of mixed feeders like red deer and fallow deer. In forest-dominated areas mixed feeders seem to be able to adopt browser-like diets and may exert competitive pressure on specialized browsers like moose. Whether the same could be true for the opposite end of the browser-to-grazer continuum is a question I could not address because no true grazers were included in my analyses. Nevertheless, feeding competition between mixed feeders and grazers seems less likely since grasses are generally fairly resistant to cropping by foragers and can rapidly regenerate from their basal meristems (Skarpe & Hester, 2008). This can even promote facilitative relationships between grazers and other feeding types. For example, red deer have been shown to prefer swards of grass that were previously grazed by cattle (Gordon, 1988). In the context of multispecies communities, behavioural interactions between species may also be important. For example, interference competition on feeding sites has been reported for roe deer and fallow deer with the latter being dominant during interactions (Ferretti *et al.*, 2011).

The use of molecular techniques for species identification showed that misidentification rates were highest between ungulates that belonged to the same family and were of similar body size. This raises concern about the accuracy of visual or morphometry-based species identification of dung samples in such multispecies communities. While observer experience did improve identification success it could not compensate for the fundamental problem of interspecific overlap in dung morphometry between similarly sized species. The practical implications of these results for monitoring ungulates largely depend

on the objectives of researchers and managers. For example, the widely used pellet groups counts would still be reliable if focused on species with clearly distinguishable dung morphology such as moose. In some instances, it might also be sufficient to summarize pellet groups from similar species into a density index. If, however, species level identification is necessary like in dung-based diet studies, DNA testing should be employed to verify the species. If the monitoring of abundance or population dynamics is the objective, camera trapping could be considered as an alternative to pellet counts, particularly for smaller species like roe deer and fallow deer which are prone to the highest rates of misidentification in pellet group counts. While misidentification can still be a problem with camera traps, the challenge typically lies in recognizing individuals and not species. For example, in a camera trap study on four deer species in Sweden, Pfeffer *et al.* (2018) could not identify the species in only 8% of the capture events.

The proportion of graminoids in the observed diets for red deer and fallow deer were lower than expected for mixed feeders and rarely exceeded 15%. It cannot fully be ruled out that these results may stem from an unknown source of bias during DNA extraction or PCR amplification steps (Nichols *et al.*, 2018). The relative differences between the species, however, agreed well with expectations based on feeding type; i.e., showing the highest proportions of graminoids for fallow deer and the lowest for moose diets. In the context of graminoid utilization by grazing-adapted ruminants, some interesting results were recently reported by Kowalczyk *et al.* (2019) for European bison in the Bialowieza forest of Poland. Using a DNA metabarcoding approach very similar to my own, they found that graminoids represented only 4% (compared to 34% forbs and 59% woody species) of DNA reads in bison diets during the months from April to November. Diets containing low proportions of graminoids and high proportions of browse could thus simply be an adaption of mixed feeders to forest-dominated landscapes. These findings could, of course, also be viewed as further evidence of a possible bias against graminoids. However, other metabarcoding studies using the same chloroplast (trnL) marker did detect high proportions of graminoids in ungulate diets when expected (e.g., Kartzinel *et al.* (2015), Pansu *et al.* (2019), and Scasta *et al.* (2019)); in my own data, high proportions of graminoids were also detected in individual samples (e.g., maxima of 66% for red deer and 71% for fallow deer during autumn) .

Like any other method to identify diets, DNA metabarcoding may be prone to some biases but their effect would almost certainly be consistent across samples. While the absolute proportions of food items presented as RRA in this thesis should be interpreted with some caution, relative differences (e.g., dietary differences between seasons, species, or dietary overlap) are likely to be true

ecological signals. For example, the diet profiles based on RRA corresponded well with generally known diet patterns such as increasing pine utilization by moose during winter, and the increased use of other food items like birch and willow in areas such as the Swedish mountains where we know pine is not available (Appendix 1c).

Intraspecific dietary variation *V* was largely consistent with my predictions. All four deer species showed the same unimodal seasonal pattern of lower *V* during spring and winter, and higher values for summer and autumn. This could be a result of the greater diversity of available forage during the latter two seasons, which could result in more diversified diets among individuals. *V* was higher among the smaller deer species than in moose which could be due to the smaller species frequenting a wider range of habitat types, including close proximity to urban areas, open fields and forest edges where they were likely to encounter a wide range of forage items (Marchal *et al.*, 1998; Borkowski & Pudełko, 2007; Lande *et al.*, 2014). Moose, on the other hand, tend to avoid agricultural areas (Olsson *et al.*, 2011). Pansu *et al.* (2019) found muzzle width to be a good predictor of *V* with narrow-muzzled species showing higher values of *V*. This is supported by the low values of *V* for moose. Moose possess a broad muzzle and have been shown to forage rather indiscriminately (Shipley *et al.*, 1998), aiming for maximizing dry-matter intake with their bites (Haukioja & Lehtilä, 1992). Smaller species with narrow muzzles like roe deer are more adapted to select forage at a much finer spatial scale (Janis & Ehrhardt, 1988), promoting inter-individual variation of diets.

Despite seasonal changes in the composition of diets, overall dietary niche width (DNW), surprisingly, did not vary much from one season to another. These results are comparable to observations by Redjadj *et al.* (2014) who reported large changes in diet composition but not in DNW for autumn and winter diets of red deer, roe deer, mouflon (*Ovis ammon*), and chamoix (*Rupicabra rupicabra*) in the French Alps. Similarly, my initial prediction that the mixed feeders, red and fallow deer, would show considerable seasonal switches from woody browse during winter to mostly forbs and grasses during the vegetation season was only weakly supported. Although grass and forbs increased in their diets during summer and autumn, the proportion of woody forage also remained high at approximately 50%. For red deer, broadleaf forage even exceeded forbs and grasses in the diet from July to September. I also detected surprisingly large proportions of forbs and graminoids during winter and early spring in the diets of the three smaller deer species which may have been a result of supplementary feeding. The provision of supplementary food was not uncommon in the study area and frequently consisted of locally produced hay or silage, containing the same plant species as the natural

vegetation. I could therefore not distinguish between intakes of supplementary food and plants that may have been foraged under the snow. The proportion of arable land (which may have a link to supplementary feeding) had a positive effect on DNW for moose, red deer and fallow deer but a mere increase in DNW does not necessarily indicate a 'better', i.e., nutritionally optimal diet (Edwards, 1983; Felton *et al.*, 2017; Felton *et al.*, 2018).

Interspecific dietary overlap tended to be lowest during summer and autumn when the diversity of available plants was highest except for moose and red deer which showed the highest overlap during summer and autumn. A possible explanation could be the high proportions of broadleaves in the diets of both species during those seasons. Feeding competition over deciduous forage during the vegetation season could potentially lead to increased summer browsing by moose on pine. Support for this hypothesis is offered by findings of Nichols and Spong (2014). Using DNA analysis of browsing bites on twigs, they showed that in a southern Swedish area with increasing numbers of red deer, the majority of the summer browsing damage to pine could still be attributed to moose (74%). Dietary overlap also declined with increasing proportions of arable land for the species pairs moose-fallow deer and moose-red deer during summer. As mixed feeders, the two smaller species were probably better adapted than moose to exploit grasses and forbs associated with agrarian areas. For moose, intraspecific dietary overlap was higher than interspecific overlap with any of the other three species (see Figure 10). For the smaller deer species, intraspecific dietary overlap was generally similar to interspecific overlap. This suggests that moose occupies a more separate dietary niche and might potentially compete more with conspecifics than the other deer species. The latter could, however, intensify such a process.

Ecological theory predicts that under conditions of competition, species will increasingly specialize on resources they can utilize exclusively (Anderwald *et al.*, 2016). Such a mitigating response was suggested by my results for the resource partitioning between moose and the smaller deer species over *Vaccinium* spp. in the field layer. In areas of high deer density, moose diets contained less *Vaccinium* spp. and higher proportions of pine compared to areas of medium and low deer densities. The availability of pine could not explain this pattern, since pine was least available in areas of high deer density. In other words, the foraging of smaller deer species in the field layer appeared to drive moose to switch towards greater consumption of pine. Food availability measurements indicated that on transects with high deer density, total abundance (i.e., volume) of *Vaccinium* spp. might have been lower and its distribution patchier than in areas with fewer deer. One could also expect dwarf shrubs to be shorter as a result of the high browsing pressure. I did not measure the height of

the field layer but personal observations and comments from field personnel supported these suppositions. Similar effects on the field layer have been shown in North American studies on white-tailed deer densities (Rossell *et al.*, 2005; Rooney, 2009). In Norway, Melis *et al.* (2006) found reductions in bilberry cover by 60% due to red deer browsing. Feeding on patchy, heavily browsed *Vaccinium* spp. shrubs would increase search time and presumably offer only small bites. According to the hypothesis of bite-size driven resource partitioning, this would reduce the attractiveness to moose and prompt them to switch to higher foraging strata offering larger bites - exactly what was suggested by the observed increase in pine consumption. Moreover, the choice of pine by moose as an alternative bulk food to *Vaccinium* spp. fits well with the bite-size hypothesis because bites of pine have been found to contain more biomass than those on deciduous species (Hagen, 1958; Cederlund *et al.*, 1980). An aspect that requires further study is whether a change in the pine and *Vaccinium* spp. proportions in the diet has any long-term repercussions for the well-being and fitness of moose. The observed switch to pine may also have important implications for the forestry-moose conflict. To minimize moose browsing damage on pine, managing key food items like *Vaccinium* spp. and controlling populations of the smaller deer (Pfeffer *et al.*, 2019) might be of equal or even greater importance than simply reducing the number of moose.

This also applies to ungulate management beyond moose. Ungulate species should not be managed in isolation but be recognized as important 'ecosystem engineers' (Smit & Putman, 2011). To ensure their continued widespread presence in Sweden and beyond, particularly in the context of environmental, economic, and societal challenges, ungulates should be viewed as an opportunity and valuable renewable resource rather than a nuisance (Apollonio *et al.*, 2017).

# 5 Conclusions

Based on the research presented in this thesis, I conclude that:

- Hofmann's hypothesis of ruminant feeding types provides a useful starting point for investigating trophic relationships in multispecies ungulate communities. Mixed feeders like red deer and fallow deer appear to possess larger dietary plasticity than browsers like moose or roe deer. Increases of mixed feeders in areas previously dominated by browsers may result in feeding competition that more strongly affects the latter.
- Species identification of faecal pellets from similar-sized ungulates via dung morphometry is difficult. In areas where such species coexist, and monitoring is aimed at the whole community, the accuracy of pellet group counts as a monitoring tool is questionable. DNA testing or camera traps may be better alternatives for this increasingly common situation across Europe. Pellet group counts remain useful if communities contain only species with clearly different dung morphometry such as moose and roe deer.
- Intraspecific dietary overlap for moose is higher than interspecific dietary overlap with either of the three smaller deer species. Among-individual dietary variation *V* was also lower for moose than for the other species. The dietary niche of moose expanded into utilization of pine and juniper which were rarely consumed by the other deer species. This suggests that for moose the potential for intraspecific competition over food items might currently be greater than the potential for competition with other deer species. The possible additive and indirect effects of the latter, however, need to be carefully examined.
- In Sweden, red deer and fallow deer appear to have adopted a 'forest-type' diet with high proportions of browse throughout the year. Ericaceous shrubs like *Vaccinium* spp. are a particularly important food source also for roe deer and moose. In areas of high deer density, moose consumed less *Vaccinium*

spp. and higher proportions of pine. This suggests feeding competition between moose and the smaller deer species over *Vaccinium* spp. in the field layer which drives moose towards increased pine browsing. For mitigating the forestry-moose conflict over browsing damage to pine, managing key food items (like *Vaccinium* spp.) and controlling the populations of the smaller deer might be of equal or even greater importance than simply reducing the number of moose.

- DNA metabarcoding proved to be a suitable tool for the processing of large sample numbers from multiple species. The simultaneous identification of ungulate species and diet composition from eDNA samples is an advantage that molecular methods have over alternatives such as microhistology. Despite some possible biases, the DNA-based diet data yielded ecologically credible results. Moreover, the data can be directly compared to or/and combined with additional DNA metabarcoding studies as long as the same markers and laboratory procedures are used which promotes collaboration with other research groups.

# 6 Future research

Conducting research frequently feels reminiscent of disassembling Russian Matryoshka dolls with each answer just revealing yet another question hidden inside. From the work carried out in the course of this PhD, some immediate and broader research questions have emerged. I will start by addressing the immediate ones:

First, the observed partitioning between moose and the smaller deer species over *Vaccinium* spp. should be further investigated to confirm if the higher proportions of pine in moose diets in areas of high deer densities also correspond to higher levels of browse damage. The physical and chemical properties of *Vaccinium* spp. in areas of high and low ungulate densities should be measured to clarify which aspects may prompt moose to switch to pine. Is it patchiness and reduced bite size as I hypothesized or are possible changes in the chemical / nutritional composition (Moe *et al.*, 2018) also important? Which deer species exerts the strongest browsing impact on *Vaccinium* spp.? Are there thresholds that predict which level(s) of *Vaccinium* spp. modification induce moose to switch to pine?

Second, is the high dietary overlap between moose and red deer during the growing season indeed linked to shared utilization of broadleaves and if yes, which species? Does this lead to resource partitioning and to which alternative food items does either species switch?

Third, what are the nutritional properties of the food items identified in ungulate diets? Are plant taxa nutritionally interchangeable or complementary, i.e., is the nutritional composition of diets perhaps even more informative than the taxonomic? As the latter is easier to determine, can it be used to reliably infer the former? The DNA metabarcoding approach has produced a data set that may be large enough to apply association rule mining to ungulate diets to search for stable associations between individual food items. These may reveal novel insights into ‘optimal diets’.

Fourth, analyses should be expanded to include ungulate diets from the other European sites. The increased gradients in landscape composition, climate and ungulate community composition would enable more comprehensive analyses, particularly with regard to intraspecific dietary plasticity. This 'EuroDiet' data set also includes grazers like horses and cattle which would allow for further testing of Hofmann's feeding types and facilitate investigations of trophic interactions along the whole browser-to-grazer continuum. One specific question which Pansu *et al.* (2019) already addressed for African ungulate communities, is the relationship between *V* and DNW, i.e., do species with higher *V* also show larger DNW?

For the most part, my investigations of resource use and partitioning among ungulates have been restricted to diets. A species' realized niche, however, has more dimensions and partitioning can also occur on spatial and temporal scales. For example, Putman (1996) showed that combining measures of dietary overlap and overlap in habitat use reduced the overall niche overlap between ungulates. Future research should aim at incorporating these aspects, which would provide a more comprehensive insight into the potential for competition. To fully examine the latter, long-term monitoring of niche overlaps in combination with data on condition and fitness are needed. The role of supplementary feeding and other anthropogenic modifications of the foodscape are of particular importance in this context.

Negative effects of environmental changes such as global warming on important aspects of ungulate foraging and other behaviours can be amplified by interspecific competition (Mason *et al.*, 2014). Future studies should aim to link trophic resource use and partitioning of ungulates to the many recent trends and processes characteristic of Europe's novel ecosystems, for example, the return of large carnivores (Chapron *et al.*, 2014) and (trophic) rewilding (Jepson, 2016; Cromsigt *et al.*, 2018).

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# Popular science summary

Over the past decades, ungulates (animals with hooves) throughout the northern hemisphere have strongly increased in numbers and range. In Europe, deer species like moose, roe deer, red deer, and fallow deer have been especially successful, with population sizes more than doubling since the 1960s. Areas in which ungulates were once scarce, or where only few species occurred, are now frequently transforming into rich multispecies systems.

While this is often celebrated as a conservation success, there are also challenges associated with such a strong recovery. High numbers of ungulates can mean increasing levels of impacts on resources that are of economic value to humans such as timber trees or agricultural crops, rising numbers of vehicle collisions with wildlife, and greater risks of transmitting diseases to livestock or humans. Managing such human-ungulate conflicts can be difficult, especially in situations where we have no historic examples for guidance, and where it is unknown how ungulate species in the newly formed communities will interact with each other and their environment. The high level of uncertainty in such 'novel ecosystems' is often addressed through adaptive management which incorporates a strategy of constant system monitoring and learning with the aim of reducing uncertainty over time.

In this thesis, I investigated what moose, roe deer, red deer, and fallow deer eat throughout the year in different landscapes and how they might affect one another through their food choices in Sweden as well as at the European scale. To determine their diets, I synthesized data from the literature and used DNA metabarcoding on dung pellets. DNA metabarcoding is a technique which, based on the DNA sequences extracted from a dung sample, allowed me to identify both the deer species, and which plants the animal had consumed.

I found that it is difficult to correctly identify which deer species dung pellet groups belonged to, based on appearance and size (dung morphometry) alone. The DNA results showed that in areas where similar-sized ungulates coexist, dung pellets are often misclassified in the field. For example, fallow deer pellets

were frequently mistaken as roe deer or red deer. This questions the reliability of pellet group counts as a monitoring technique for deer populations in such systems. Moose pellets, however, could clearly be distinguished from other deer species due to their substantially bigger size.

When it comes to diets, ruminants (which include all the deer species) are generally believed to belong to different feeding types ranging from browsers (eating mostly woody vegetation and forbs) to grazers (eating grass) with mixed feeders (able to switch between browsing and grazing) in between. Moose and roe deer are usually classified as browsers whereas red and fallow deer are mixed feeders with fallow deer typically being viewed as the most grazer-like of the European deer species. On the continental scale, the average diets of these four main European deer species fit well with those feeding types. The mixed feeders, red and fallow deer, showed larger dietary plasticity than moose and roe deer as browsers.

The adaptability of mixed feeders to different food sources was also supported by the DNA-based diet data. In the forest-rich landscapes of Sweden, red and fallow deer foraged more like browsers with substantial proportions of woody plant species in their diet. The overall number and proportions of food items consumed by a species is referred to as its dietary niche width; specialized species have narrower niches than generalist. As could be expected for a specialized browser, dietary niche width was lowest for moose while it was highest for mixed-feeding fallow deer. The extent to which animals use the same food resources is referred to as dietary niche overlap. Such niche overlap can be described as intraspecific (between individuals of the same species) and interspecific (between individuals belonging to different species). For moose, intraspecific dietary overlap was higher than dietary overlap with either of the smaller deer species.

Dwarf shrubs in the forest field layer such as bilberry and lingonberry (*Vaccinium* spp.) comprised a major component in the diet of all four deer species throughout the year. Moose diets also contained larger proportions of Scots pine during winter and spring than those of the other deer species. In areas with high densities of the smaller deer, moose, but not the other deer species, consumed more pine and less *Vaccinium* spp. This suggests that feeding competition from the smaller deer species over *Vaccinium* spp. may push moose towards eating more pine instead. This could potentially exacerbate the forestry-moose conflict over damage to commercially valuable pine.

In order to alleviate such negative impacts, assuring sufficient abundance and optimal growing conditions for key food items like *Vaccinium* spp. and managing the populations of smaller deer species may be of equal or greater importance than a simply reducing the number of moose. Future research should

focus on the nutritional dimension of changes in ungulate diets and investigate possible ramifications for their well-being and fitness.

# Populärvetenskaplig sammanfattning

Under de senaste decennierna har stammarna av klövvilt vuxit på norra halvklotet, samtidigt som arterna utökat sina utbredningsområden. I Europa har älg, rådjur, kronhjort och dovhjort varit särskilt framgångsrika, med stammar som idag är mer än dubbelt så stora som på 60-talet. I områden som tidigare hade ett fåtal individer av enstaka arter förekommer nu ofta individrika flerartssystem. Förändringen visar på en stor framgång för naturvårdsarbetet och viltförvaltningen, men innebär samtidigt utmaningar. Täta klövviltstammar medför ökad risk för skador på skog och grödor, fler viltolyckor i trafiken och ökad risk för att vilt sprider sjukdomar till tamboskap och människor. Det kan vara en utmaning att hantera de konflikter som starka klövviltstammar medför, speciellt i de fall där det saknas praktisk erfarenhet av hur nya klövviltsamhällen fungerar och interagerar med den miljö där de lever. Osäkerheten inom förvaltningen av sådana nya flerartssystem hanteras ofta genom ”adaptiv” förvaltning, där mål, åtgärder och verkan utvärderas kontinuerligt över tid för att öka måluppfyllnaden.

I den här avhandlingen har jag undersökt vad älg, rådjur, kronhjort och dovhjort äter under året i olika typer av landskap i Sverige och Europa, och hur hjortarterna påverkar varandra genom sina foderval. För att fastställa dietvalet har jag dels gått igenom den vetenskapliga litteraturen, dels utfört analyser av de DNA-rester från födoväxter som finns i spillningen från hjortdjur. Samtidigt analyserade jag även vilken hjortart spillningen kom ifrån.

Därmed kunde jag utvärdera spillningsinventering som metod, genom att validera visuell artbestämning med DNA-analyser. Jag fann att det var svårt att korrekt fastställa vilken art spillning kom från baserat på storlek och utseende på spillningen, utom för älg. Resultaten visar att det inte går att särskilja rådjur, dovhjort och kronhjort med god precision, vilket begränsar användbarheten av spillningsinventeringar i flerartssystem.

Idisslare brukar delas in kvalitetsbetare (äter huvudsakligen vedartad växtlighet och örter), selektiva blandätare (kan växla mellan kvistbete och

mulbete) samt gräs- och grovfoderätare (äter huvudsakligen gräs). Min sammanställning av befintlig litteratur visar att älg och rådjur framför all är kvalitetsbetare medan kronhjort och dovhjort är selektiva blandätare. Dovhjorten är typiskt den av våra hjortarter som ligger närmast mulbete. Kronhjort och dovhjort var mer plastiska än älg och rådjur, och hade en större andel kvistbete i norra än i centrala Europa.

De selektiva blandätarnas flexibilitet i foderutnyttjande avspeglade sig även i mina DNA-analyser av diet från spillning. I Sverige, som är skogsdominerat, utnyttjade kron- och dovhjort kvistbete i större utsträckning än i Centraleuropa. Antalet olika foderarter och deras andel i dieten utgör en växtätares ”nischbredd”, där specialiserade arter har en smalare nisch än generalister. Nischbredden var som förväntat smalast för den mer specialiserade älgen och bredast för dovhjorten som är en selektiv blandätare. Nischöverlappet mellan individer utrycker i vilken utsträckning de utnyttjar samma foderväxter. För älg var nischöverlappet inom arten större än överlappet mellan älg och övriga hjortarter.

Bärris i skogens fältskikt, som blåbär och lingon, utgjorde en stor andel av födan under hela året för alla hjortarter som undersöktes, medan älgdieten innehöll en större andel tall under vinter och vår jämfört med de övriga hjortarterna. I områden med täta stammar av de mindre hjortarterna åt älgar mer tall och mindre bärris, medan samma mönster saknades för de mindre arterna. Detta antyder att konkurrens från de mindre hjortarterna kan tvinga älgen att äta mer tall, vilket kan öka skogsskadorna.

För att minska skadorna på tall kan det vara mer effektivt att anpassa skogsskötseln för att gynna bärris och att reglera antalet mindre hjortdjur, än att enbart fokusera på att reglera tätheten på älgstammen. Framtida forskning bör fokusera på näringsvärdet i olika dieter för olika klövvilt, och vilken inverkan det har på klövviltsstammarnas kvalitet och individernas välmående.

# Acknowledgements

Rumour has it that this last section is often read first, and rightfully so. Arriving at this point in my academic career would not have been possible without the help of many wonderful people.

I want to start by thanking my main supervisor, Joris Cromsigt, for having given me the opportunity to embark on this journey of discovery over the past four years. Your guidance and solution-oriented approach to challenges along the way have truly been invaluable. I particularly admire your ability to handle multiple projects simultaneously.

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At the lab in Umeå, I am particularly indebted to Helena Königsson. Helena, the importance of your helpful, patient and encouraging attitude during my long weeks of DNA extractions cannot be overstated.

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There is some truth to the saying that teamwork divides the tasks and multiplies success, so I am thankful to all my colleagues at the Department of Wildlife, Fish, and Environmental Studies for creating a pleasant and stimulating work environment.

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No one can probably relate to PhD life quite as well as those still in it, which is why my fellow PhD students (past and present) have been an invaluable source of support and inspiration. Andy, it has been great sharing the office with you during the first year and to see you move on to a postdoc on your dream topic. Martijn, thanks for the great help with all the thesis technicalities on the final leg to the finish line. Chris, I could not have wished for a better officemate; I

appreciate your sense of humour, your eye for details and your ability to produce beautiful maps (Bauhaus colours!) - and thanks for turning our office into something of a spa on occasion. Sabrina, you are a paragon of organization and usually the best person to ask how things work, thank you for that. You are up next, and you will no doubt do great! Sabine, it was delightful to see you continuing from your Master's into a PhD and I hope we will collaborate again in the future. To all other staff and students that I had the pleasure of meeting at SLU and beyond – thank you! I would also like to acknowledge the many anonymous contributors to such sites as stackoverflow.com who invested the time to post solutions to nearly any coding problem imaginable.

There was, of course, also still (a bit of) a life left outside the PhD work; I especially want to thank Alisa and Magnus for their hospitality during my frequent visits to Jokkmokk. Magnus, our hunting trips went a long way towards preserving my sanity over these past years! ;)

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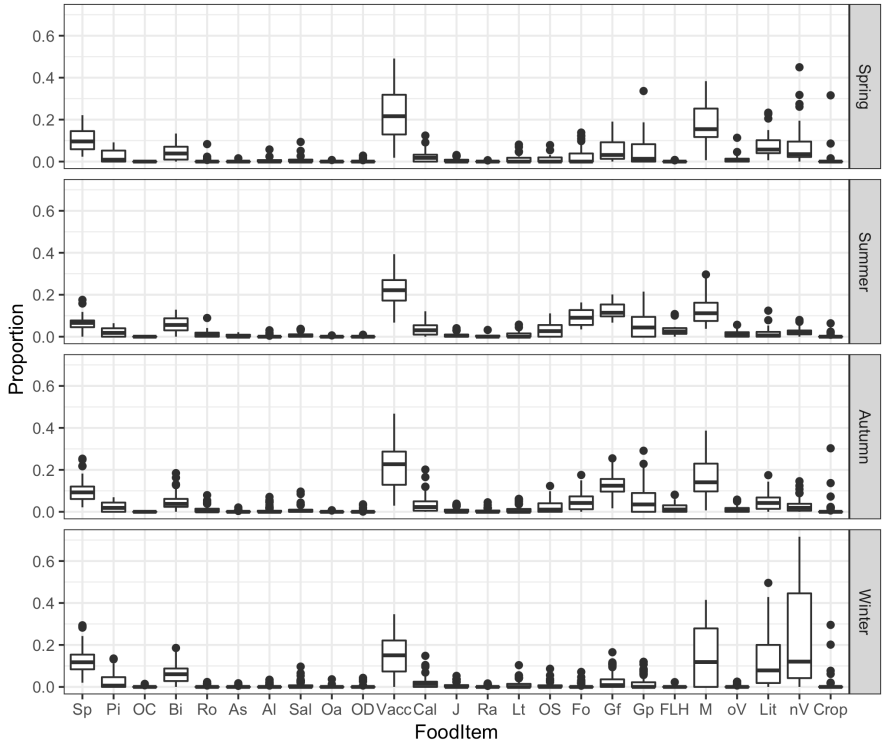
To those who are closest to me only few words are needed. Mutti, Vati and Jakob, you have known me the longest and you know how irreplaceable your support has always been. To my family in New York and Guyana, thank you for being a home away from home; I am not sure I could have finished without the recharging visits.

Finally and above all, I thank my lovely wife Clydecia. You are the one who knows me best and you have been an unwavering support along every stage of this emotional rollercoaster ride. You make it all worth it.

Umeå, 9 November 2019.

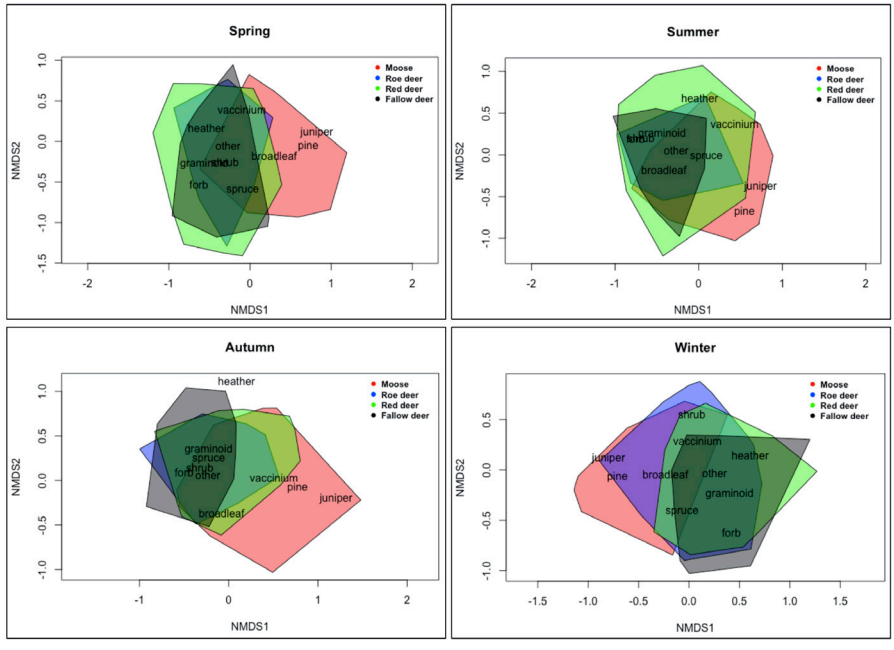
# Appendix 1: Additional figures

## 1a) Food availability on transects



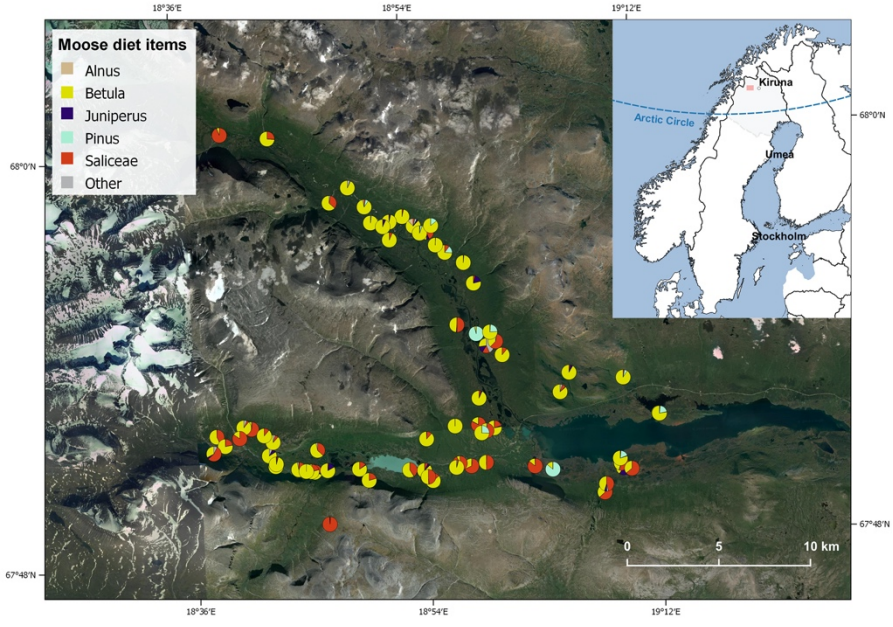

*Appendix 1a.* Food availability in the study area during different seasons. Data from the Nordmaling and Öster Malma sites has been combined (Sp = spruce, Pi = pine, OC = other conifers, Bi = birch, Ro = rowan, As = aspen, Al = alder, Sal = willow, Oa = oak, OD = other hardwood, Vacc = *Vaccinium* spp., Cal = heather, J = juniper, Ra = raspberry, Lt = labrador tea, OS = other shrub, Fo = forb, Gf = graminoid (in forest), Gp = graminoid (in pasture), FLH = fern/lycopod/horsetail, M = moss, oV = other vegetation (e.g., lichen), Lit = litter, nV = non-vegetation (e.g., rock surface or snow), Crop (on agricultural fields).

## 1b) NMDS ordination of deer diets



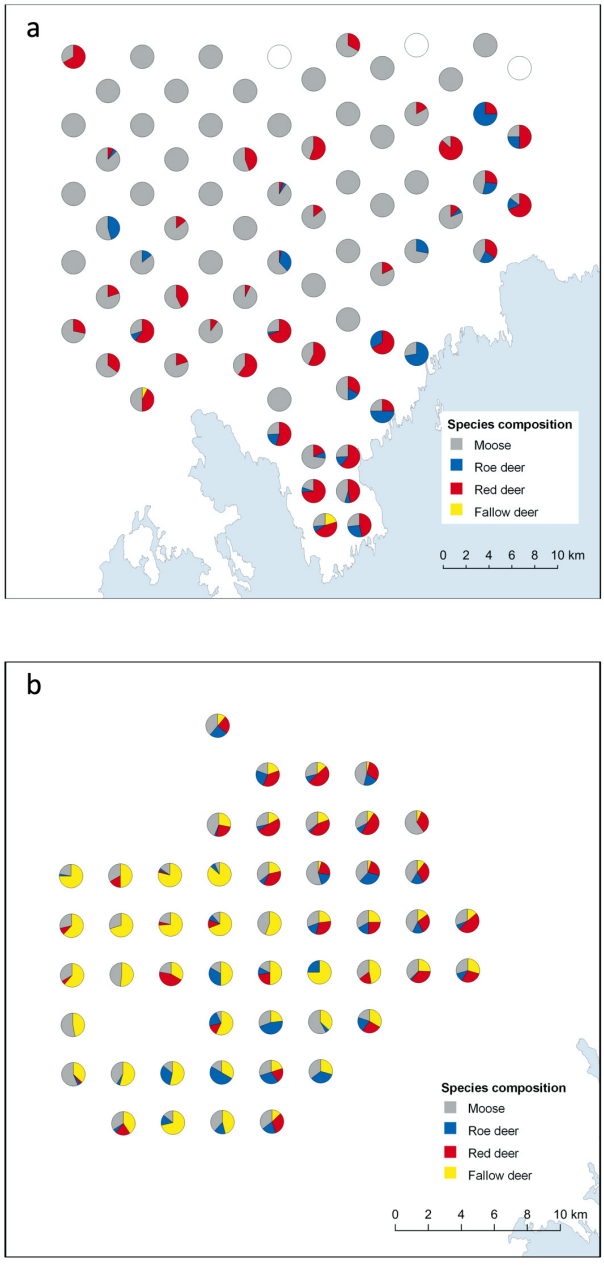

*Appendix 1b.* Non-metric dimensional scaling (NMDS) ordination of Bray-Curtis dissimilarity of diets among four deer species during different seasons and projection of 10 main food items. For better visibility, only minimum convex polygons (convex hulls) instead of individual faecal samples are shown for each species (indicated by colour). Dietary niches of the four species largely overlap with moose separating the most due to utilization of pine and juniper.

## 1c) Moose winter diets in the mountains of northern Sweden




*Appendix 1c.* Moose winter diets in the mountains of northern Sweden (Nikkaluokta). Each pie chart corresponds to a faecal sample that was collected from a live, tranquilized animal as part of a study on movement and metabolomics (Resource Extraction and Sustainable Arctic Communities (REXSAC), https://www.rexsac.org/). Faecal samples were processed alongside the samples used in thesis, using exactly the same DNA metabarcoding protocols. Diet composition has been aggregated into 6 categories. The observed diets reflect the local food availability which in winter is almost completely restricted to birches (*Betula* spp.) and willows (Saliceae). The occasional high proportions of pine (*Pinus sylvestris*) in diets (e.g., near the centre of the map) correspond to known, isolated stands of pine in the area.

1d) Proportions of faecal samples for four deer species at transect scale




*Appendix 1d.* Proportions of DNA-verified faecal samples of four deer species (indicated by colours, empty circles correspond to no data) for each transect at the Nordmaling (a) and Öster Malma (b) sites.

# Appendix 2: Diet summaries

Appendix 2a. *Overview of MOTUs (N = 207) identified in Swedish deer diets with best taxonomic assignment and rank, corresponding plant family (or higher taxonomic rank), and functional group (i.e., growth form/food category).*

| MOTU No. | Best assignment | Taxrank | Family (or higher) | Functional group | Functional group 2[a] |
|---|---|---|---|---|---|
| 1 | *Abies* | genus | Pinaceae | conifer | other |
| 2 | *Acer* | genus | Aceraceae | broadleaf | broadleaf |
| 3 | *Achillea millefolium* | species | Asteraceae | forb | forb |
| 4 | *Aegopodium* | genus | Apiaceae | forb | forb |
| 5 | *Agrimonia eupatoria* | species | Rosaceae | forb | forb |
| 6 | Agrostidinae | subtribe | Poaceae | graminoid | graminoid |
| 7 | *Alchemilla* | genus | Rosaceae | forb | forb |
| 8 | *Alnus* | genus | Betulaceae | broadleaf | broadleaf |
| 9 | *Alnus alnobetula* | species | Betulaceae | broadleaf | broadleaf |
| 10 | *Alopecurus geniculatus* | species | Poaceae | graminoid | graminoid |
| 11 | *Andromeda polifolia* | species | Ericaceae | shrub | shrub |
| 12 | *Anemone* | genus | Ranunculaceae | forb | forb |
| 13 | Anthemideae | tribe | Asteraceae | forb | forb |
| 14 | Apioideae | subfamily | Apiaceae | forb | forb |
| 15 | *Arabis alpina* | species | Brassicaceae | forb | forb |
| 16 | *Arctostaphylos uva-ursi* | species | Ericaceae | shrub | shrub |
| 17 | Asteraceae | family | Asteraceae | forb | forb |
| 18 | Asterales | order | Asterales | forb | forb |
| 19 | Asteroideae | subfamily | Asteraceae | forb | forb |
| 20 | *Aulacomnium* | genus | Aulacomniaceae | moss | other |
| 21 | *Avena* | genus | Poaceae | graminoid | graminoid |
| 22 | *Avenella flexuosa* | species | Poaceae | graminoid | graminoid |
| 23 | Aveninae | subtribe | Poaceae | graminoid | graminoid |
| 24 | *Beta vulgaris* | species | Chenopodiaceae | crop | other |
| 25 | *Betula* | genus | Betulaceae | broadleaf | broadleaf |

| MOTU No. | Best assignment | Taxrank | Family (or higher) | Functional group | Functional group 2[a] |
|---|---|---|---|---|---|
| 26 | Betulaceae | family | Betulaceae | broadleaf | broadleaf |
| 27 | *Bistorta vivipara* | species | Polygonaceae | forb | forb |
| 28 | Brachytheciaceae | family | Brachytheciaceae | moss | other |
| 29 | *Brassica oleracea* | species | Brassicaceae | crop | other |
| 30 | Brassicaceae | family | Brassicaceae | forb | forb |
| 31 | *Bryonia dioica* | species | Cucurbitaceae | shrub | shrub |
| 32 | *Bryum* | genus | Bryaceae | moss | other |
| 33 | *Calluna vulgaris* | species | Ericaceae | shrub | heather |
| 34 | *Cannabis sativa* | species | Cannabaceae | forb | forb |
| 35 | Carduinae | subtribe | Asteraceae | forb | forb |
| 36 | *Carex* | genus | Cyperaceae | graminoid | graminoid |
| 37 | *Carum carvi* | species | Apiaceae | forb | forb |
| 38 | *Chamaedaphne calyculata* | species | Ericaceae | shrub | shrub |
| 39 | *Chamaenerion angustifolium* | species | Onagraceae | forb | forb |
| 40 | *Chenopodium* | genus | Amaranthaceae | forb | forb |
| 41 | *Chenopodium suecicum* | species | Amaranthaceae | forb | forb |
| 42 | *Cirsium arvense* | species | Asteraceae | forb | forb |
| 43 | *Comarum palustre* | species | Rosaceae | forb | forb |
| 44 | *Cornus suecica* | species | Cornaceae | forb | forb |
| 45 | *Corydalis solida* | species | Papaveraceae | forb | forb |
| 46 | *Crepidinae* | subtribe | Asteraceae | forb | forb |
| 47 | *Dactylis glomerata* | species | Poaceae | graminoid | graminoid |
| 48 | *Dryopteris* | genus | Dryopteridaceae | FLH | other |
| 49 | *Empetrum* | genus | Ericaceae | shrub | shrub |
| 50 | *Epilobium* | genus | Onagraceae | forb | forb |
| 51 | Ericaceae | family | Ericaceae | shrub | shrub |
| 52 | *Eriophorum* | genus | Cyperaceae | graminoid | graminoid |
| 53 | Eudicotyledons | clade | Eudicots | other | other |
| 54 | *Euphorbia palustris* | species | Euphorbiaceae | forb | forb |
| 55 | *Fagus sylvatica* | species | Fagaceae | broadleaf | broadleaf |
| 56 | *Fallopia* | genus | Polygonaceae | other | other |

| MOTU No. | Best assignment | Taxrank | Family (or higher) | Functional group | Functional group 2[a] |
|---|---|---|---|---|---|
| 57 | *Filipendula ulmaria* | species | Rosaceae | forb | forb |
| 58 | *Filipendula vulgaris* | species | Rosaceae | forb | forb |
| 59 | *Frangula alnus* | species | Rhamnaceae | shrub | shrub |
| 60 | *Galium* | genus | Rubiaceae | forb | forb |
| 61 | *Geranium* | genus | Geraniaceae | forb | forb |
| 62 | *Geranium robertianum* | species | Geraniaceae | forb | forb |
| 63 | *Geum* | genus | Rosaceae | forb | forb |
| 64 | *Glyceria* | genus | Poaceae | graminoid | graminoid |
| 65 | *Glycine max* | species | Fabaceae | crop | other |
| 66 | Gnaphalieae | tribe | Asteraceae | forb | forb |
| 67 | *Gypsophila* | genus | Caryophyllaceae | forb | forb |
| 68 | *Hedera helix* | species | Araliaceae | shrub | shrub |
| 69 | *Helianthemum nummularium* | species | Cistaceae | forb | forb |
| 70 | *Heuchera richardsonii* | species | Saxifragaceae | forb | forb |
| 71 | Hippocastanoideae | subfamily | Sapindaceae | other | other |
| 72 | *Hippophae rhamnoides* | species | Elaeagnaceae | shrub | shrub |
| 73 | *Holcus* | genus | Poaceae | graminoid | graminoid |
| 74 | *Hordeum* | genus | Poaceae | graminoid | graminoid |
| 75 | *Hottonia palustris* | species | Primulaceae | aquatic | other |
| 76 | *Hylotelephium telephium* | species | Crassulaceae | forb | forb |
| 77 | *Hypericum* | genus | Hypericaceae | forb | forb |
| 78 | Hypnales | order | Hypnales | moss | other |
| 79 | *Iris* | genus | Iridaceae | forb | forb |
| 80 | *Juglans regia* | species | Juglandaceae | broadleaf | broadleaf |
| 81 | *Juncus* | genus | Juncaceae | graminoid | graminoid |
| 82 | *Juncus ranarius* | species | Juncaceae | graminoid | graminoid |
| 83 | *Juniperus* | genus | Cupressaceae | shrub | juniper |
| 84 | Lamiales | order | Lamiales | other | other |
| 85 | *Lathraea squamaria* | species | Orobanchaceae | other | other |
| 86 | *Lathyrus* | genus | Fabaceae | forb | forb |
| 87 | *Lathyrus pratensis* | species | Fabaceae | forb | forb |
| 88 | *Leontodon hispidus* | species | Asteraceae | forb | forb |

| MOTU No. | Best assignment | Taxrank | Family (or higher) | Functional group | Functional group 2[a] |
|---|---|---|---|---|---|
| 89 | *Ligustrum vulgare* | species | Oleaceae | shrub | shrub |
| 90 | *Limosella aquatica* | species | Scrophulariaceae | aquatic | other |
| 91 | *Linnaea borealis* | species | Caprifoliaceae | forb | forb |
| 92 | *Linum usitatissimum* | species | Linaceae | crop | other |
| 93 | *Lotus corniculatus* | species | Fabaceae | forb | forb |
| 94 | *Lupinus* | genus | Fabaceae | forb | forb |
| 95 | *Luzula* | genus | Juncaceae | graminoid | graminoid |
| 96 | *Luzula pilosa* | species | Juncaceae | graminoid | graminoid |
| 97 | Lycopodioideae | subfamily | Lycopodiaceae | FLH | other |
| 98 | *Lycopus europaeus* | species | Lycopodiaceae | forb | forb |
| 99 | *Lysimachia* | genus | Primulaceae | forb | forb |
| 100 | *Lysimachia thyrsiflora* | species | Primulaceae | forb | forb |
| 101 | *Lysimachia vulgaris* | species | Primulaceae | forb | forb |
| 102 | *Lythrum salicaria* | species | Lythraceae | forb | forb |
| 103 | *Medicago* | genus | Fabaceae | forb | forb |
| 104 | *Melampyrum pratense* | species | Orobanchaceae | forb | forb |
| 105 | *Melampyrum sylvaticum* | species | Orobanchaceae | forb | forb |
| 106 | *Mentha* | genus | Lamiaceae | forb | forb |
| 107 | Mentheae | tribe | Lamiaceae | other | other |
| 108 | *Menyanthes trifoliata* | species | Menyanthaceae | aquatic | other |
| 109 | *Mesangiospermae* | clade | Mesangiospermae | forb | forb |
| 110 | *Micranthes nudicaulis* | species | Saxifragaceae | forb | forb |
| 111 | *Myosotis arvensis* | species | Boraginaceae | forb | forb |
| 112 | *Myrica gale* | species | Myricaceae | shrub | shrub |
| 113 | Nymphaeaceae | family | Nymphaeaceae | aquatic | other |
| 114 | Oenantheae | tribe | Apiaceae | other | other |
| 115 | Oleeae | tribe | Oleaceae | broadleaf | broadleaf |
| 116 | *Orthilia secunda* | species | Ericaceae | forb | forb |
| 117 | *Oryza sativa* | species | Poaceae | crop | other |
| 118 | *Oxalis acetosella* | species | Oxalidaceae | forb | forb |
| 119 | PACMAD clade | clade | Poaceae | graminoid | graminoid |
| 120 | Pentapetalae | clade | Pentapetalae | forb | forb |

| MOTU No. | Best assignment | Taxrank | Family (or higher) | Functional group | Functional group 2[a] |
|---|---|---|---|---|---|
| 121 | *Persicaria* | genus | Polygonaceae | forb | forb |
| 122 | *Phragmites australis* | species | Poaceae | graminoid | graminoid |
| 123 | *Picea* | genus | Pinaceae | conifer | spruce |
| 124 | *Pilosella* | genus | Asteraceae | forb | forb |
| 125 | Pinaceae | family | Pinaceae | conifer | other |
| 126 | *Pinus* | genus | Pinaceae | conifer | pine |
| 127 | *Pinus contorta* | species | Pinaceae | conifer | pine |
| 128 | *Piptatheropsis pungens* | species | Poaceae | graminoid | graminoid |
| 129 | *Pisum sativum* | species | Fabaceae | crop | other |
| 130 | *Plantago* | genus | Plantaginaceae | forb | forb |
| 131 | *Plantago lanceolata* | species | Plantaginaceae | forb | forb |
| 132 | *Poa* | genus | Poaceae | graminoid | graminoid |
| 133 | Poales | order | Poales | graminoid | graminoid |
| 134 | Poeae | tribe | Poaceae | graminoid | graminoid |
| 135 | Poinae | subtribe | Poaceae | graminoid | graminoid |
| 136 | *Polygonum* | genus | Polygonaceae | forb | forb |
| 137 | Polypodiales | order | Polypodiales | FLH | other |
| 138 | *Polypodium vulgare* | species | Rosales | FLH | other |
| 139 | Pooideae | subfamily | Poaceae | graminoid | graminoid |
| 140 | *Populus* | genus | Salicaceae | broadleaf | broadleaf |
| 141 | *Potentilla* | genus | Rosaceae | forb | forb |
| 142 | *Primula* | genus | Primulaceae | forb | forb |
| 143 | *Prunus* | genus | Rosaceae | broadleaf | broadleaf |
| 144 | *Pteridium aquilinum* | species | Dennstaedtiaceae | FLH | other |
| 145 | *Pyrola* | genus | Ericaceae | forb | forb |
| 146 | *Pyrola rotundifolia* | species | Ericaceae | forb | forb |
| 147 | *Pyrus communis* | species | Rosaceae | broadleaf | broadleaf |
| 148 | *Quercus* | genus | Fagaceae | broadleaf | broadleaf |
| 149 | *Ranunculus* | genus | Ranunculaceae | forb | forb |
| 150 | *Rhinanthus* | genus | Orobanchaceae | forb | forb |
| 151 | *Rhododendron* | genus | Ericaceae | shrub | shrub |
| 152 | *Ribes* | genus | Grossulariaceae | shrub | shrub |

| MOTU No. | Best assignment | Taxrank | Family (or higher) | Functional group | Functional group 2[a] |
|---|---|---|---|---|---|
| 153 | *Rosa* | genus | Rosaceae | shrub | shrub |
| 154 | Rosales | order | Rosales | other | other |
| 155 | Rosoideae | subfamily | Rosaceae | other | other |
| 156 | Rubieae | tribe | Rubiaceae | forb | forb |
| 157 | *Rubus* | genus | Rosaceae | shrub | shrub |
| 158 | *Rumex* | genus | Polygonaceae | forb | forb |
| 159 | Saliceae | tribe | Salicaceae | broadleaf | broadleaf |
| 160 | *Salix triandra* | species | Salicaceae | broadleaf | broadleaf |
| 161 | *Sambucus* | genus | Adoxaceae | broadleaf | broadleaf |
| 162 | *Sanguisorba officinalis* | species | Rosaceae | forb | forb |
| 163 | *Sarracenia purpurea* | species | Sarraceniaceae | forb | forb |
| 164 | *Saxifraga* | genus | Saxifragaceae | forb | forb |
| 165 | *Saxifraga granulata* | species | Saxifragaceae | forb | forb |
| 166 | Scandicinae | subtribe | Apiaceae | other | other |
| 167 | *Scirpus* | genus | Cyperaceae | aquatic | other |
| 168 | *Sciuro-hypnum* | genus | Brachytheciaceae | moss | other |
| 169 | *Scorzoneroides autumnalis* | species | Asteraceae | forb | forb |
| 170 | *Securigera varia* | species | Fabaceae | forb | forb |
| 171 | *Sedum album* | species | Crassulaceae | forb | forb |
| 172 | *Sedum sexangulare* | species | Crassulaceae | forb | forb |
| 173 | Selineae | tribe | Apiaceae | other | other |
| 174 | Senecioninae | subtribe | Asteraceae | other | other |
| 175 | *Silene* | genus | Caryophyllaceae | forb | forb |
| 176 | Solanoideae | subfamily | Solanaceae | forb | forb |
| 177 | *Sparganium* | genus | Typhaceae | aquatic | other |
| 178 | *Spergula arvensis* | species | Caryophyllaceae | forb | forb |
| 179 | *Spergularia rubra* | species | Caryophyllaceae | forb | forb |
| 180 | *Sphagnum russowii* | species | Sphagnaceae | moss | other |
| 181 | *Spiraea* | genus | Rosaceae | shrub | shrub |
| 182 | *Splachnum vasculosum* | species | Splachnaceae | moss | other |
| 183 | *Stellaria* | genus | Caryophyllaceae | forb | forb |
| 184 | *Stellaria pallida* | species | Caryophyllaceae | forb | forb |

| MOTU No. | Best assignment | Taxrank | Family (or higher) | Functional group | Functional group 2[a] |
|---|---|---|---|---|---|
| 185 | Stipeae | tribe | Poaceae | graminoid | graminoid |
| 186 | *Tetraplodon pallidus* | species | Splachnaceae | moss | other |
| 187 | *Trientalis* | genus | Primulaceae | forb | forb |
| 188 | *Trifolium* | genus | Fabaceae | forb | forb |
| 189 | *Trifolium michelianum* | species | Fabaceae | forb | forb |
| 190 | *Tripleurospermum maritimum* | species | Asteraceae | forb | forb |
| 191 | Triticeae | tribe | Poaceae | graminoid | graminoid |
| 192 | *Typha* | genus | Typhaceae | aquatic | other |
| 193 | *Ulmus* | genus | Ulmaceae | broadleaf | broadleaf |
| 194 | *Urtica* | genus | Urticaceae | forb | forb |
| 195 | *Vaccinium* | genus | Ericaceae | shrub | vaccinium |
| 196 | *Vaccinium microcarpum* | species | Ericaceae | shrub | vaccinium |
| 197 | *Vaccinium ovalifolium* | species | Ericaceae | shrub | vaccinium |
| 198 | *Vaccinium oxycoccos* | species | Ericaceae | shrub | vaccinium |
| 199 | *Vaccinium uliginosum* | species | Ericaceae | shrub | vaccinium |
| 200 | *Vaccinium vitis-idaea* | species | Ericaceae | shrub | vaccinium |
| 201 | *Veronica chamaedrys* | species | Plantaginaceae | forb | forb |
| 202 | *Veronica officinalis* | species | Plantaginaceae | forb | forb |
| 203 | *Veronica serpyllifolia* | species | Plantaginaceae | forb | forb |
| 204 | *Vicia* | genus | Fabaceae | forb | forb |
| 205 | *Vicia faba* | species | Fabaceae | crop | other |
| 206 | *Vinca minor* | species | Apocynaceae | shrub | shrub |
| 207 | *Viola* | genus | Violaceae | forb | forb |

a) Functional group categories used in Paper III.

Appendix 2b. *Average relative read abundance (RAA) in percent for 207 MOTUs detected in Swedish deer diets (Aa: moose, Cc: roe deer, Ce: red deer, and Dd: fallow deer) in different seasons. The sample size (number of faecal samples for each deer species) is given in parentheses.*

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Aa (556) | Cc (143) | Ce (316) | Dd (223) | Aa (169) | Cc (15) | Ce (70) | Dd (22) | Aa (131) | Cc (35) | Ce (97) | Dd (48) | Aa (216) | Cc (135) | Ce (182) | Dd (200) |
| 1 | Abies | 0 | 0.2 | 0.2 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.2 | 0 | 0 |
| 2 | Acer | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.3 | 0 | 0.1 | 0.2 | 0.1 | 0 | 0.2 | 0 | 0.2 |
| 3 | Achillea millefolium | 0 | 0 | 0.4 | 0.5 | 0 | 0 | 0 | 0.2 | 0 | 0.1 | 0.1 | 0.2 | 0 | 0 | 0.5 | 0.6 |
| 4 | Aegopodium | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| 5 | Agrimonia eupatoria | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | Agrostidinae | 0 | 0.2 | 0.5 | 1.2 | 0 | 0.2 | 0.4 | 0.2 | 0 | 0.1 | 0.1 | 0.5 | 0 | 0 | 0.3 | 0.6 |
| 7 | Alchemilla | 0 | 0.3 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 |
| 8 | Alnus | 1 | 1 | 0.3 | 0.4 | 1.1 | 3.1 | 0.2 | 2.2 | 2.9 | 0.9 | 1.5 | 7.1 | 1.3 | 1.4 | 0.4 | 1.2 |
| 9 | Alnus alnobetula | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | Alopecurus geniculatus | 0 | 0.1 | 0.3 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0.1 |
| 11 | Andromeda polifolia | 0 | 0.1 | 0 | 0.1 | 0 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 |
| 12 | Anemone | 0 | 0.4 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | Anthemideae | 0 | 0.1 | 0.2 | 0.2 | 0 | 0 | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0.1 | 0.1 |
| 14 | Apioideae | 0 | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 | Arabis alpina | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | Arctostaphylos uva-ursi | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 1.1 | 0 | 0 | 0 | 0.2 | 0.1 | 0 |
| 17 | Asteraceae | 0 | 0.3 | 0.3 | 0.6 | 0.1 | 0 | 0.6 | 1 | 0.1 | 0.5 | 0.3 | 1.2 | 0 | 0.1 | 0.4 | 0.6 |
| 18 | Asterales | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | Asteroideae | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0.1 |
| 20 | Aulacomnium | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | Avena | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0 | 0.1 |
| 22 | Avenella flexuosa | 0 | 0.6 | 0.8 | 0.5 | 0 | 0.2 | 0.5 | 0 | 0.2 | 0.1 | 2.2 | 1.1 | 0.2 | 0.1 | 0.6 | 0.9 |
| 23 | Aveninae | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 24 | Beta vulgaris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 25 | Betula | 4.8 | 1.8 | 1.5 | 1 | 6.6 | 7.8 | 33.4 | 5.8 | 21.6 | 13.4 | 32 | 8.4 | 5.5 | 4.7 | 1.8 | 1.1 |
| 26 | Betulaceae | 0.3 | 0 | 0.1 | 0.7 | 0 | 0 | 0.1 | 0.6 | 0.1 | 0 | 0.1 | 0.4 | 0.2 | 0.5 | 0.1 | 0.2 |
| 27 | Bistorta vivipara | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 28 | Brachytheciaceae | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 29 | Brassica oleracea | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 30 | Brassicaceae | 0 | 0.1 | 0.2 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.3 |
| 31 | Bryonia dioica | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 32 | Bryum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 33 | Calluna vulgaris | 1.8 | 6.7 | 12.2 | 6.2 | 0 | 1.8 | 1 | 0.4 | 1.5 | 5.1 | 4.5 | 5.6 | 1.2 | 5.1 | 15.7 | 12.6 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 34 | Cannabis sativa | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 35 | Carduinae | 0 | 1 | 0.6 | 0.8 | 0 | 0.9 | 0.3 | 0.4 | 0 | 0.7 | 0.1 | 0.8 | 0.1 | 0.9 | 0.5 | 1.1 |
| 36 | Carex | 0 | 0.2 | 0.4 | 0.1 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 |
| 37 | Carum carvi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 38 | Chamaedaphne calyculata | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 39 | Chamaenerion angustifolium | 0 | 0 | 0 | 0 | 0.5 | 7.8 | 8.8 | 0.1 | 5.7 | 4.2 | 3.6 | 0.7 | 0 | 0 | 0 | 0 |
| 40 | Chenopodium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0.1 |
| 41 | Chenopodium suecicum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 |
| 42 | Cirsium arvense | 0 | 0.1 | 0 | 0.2 | 0 | 0 | 0 | 0.3 | 0 | 0.1 | 0 | 0.1 | 0 | 0.2 | 0.1 | 0.3 |
| 43 | Comarum palustre | 0 | 0 | 0.1 | 0 | 0 | 1.2 | 0.6 | 0 | 0 | 0.7 | 0.3 | 0.8 | 0 | 0 | 0 | 0 |
| 44 | Cornus suecica | 0 | 0 | 0 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 45 | Corydalis solida | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 46 | Crepidinae | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 47 | Dactylis glomerata | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 |
| 48 | Dryopteris | 0 | 0.8 | 1.7 | 0.2 | 0 | 0.9 | 0.7 | 0.1 | 0.1 | 0.1 | 0.8 | 0.2 | 0 | 0.4 | 1 | 0.4 |
| 49 | Empetrum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 50 | Epilobium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.9 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| 51 | Ericaceae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 52 | Eriophorum | 0 | 0.1 | 0.2 | 0 | 0 | 2.1 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 53 | Eudicotyledons | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 54 | Euphorbia palustris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 55 | Fagus sylvatica | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 |
| 56 | Fallopia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.5 | 0 | 0 | 0 | 0 |
| 57 | Filipendula ulmaria | 0 | 0.7 | 0.6 | 2 | 0.1 | 4.9 | 1.6 | 5.9 | 0.1 | 3.9 | 1.4 | 3.5 | 0 | 0.3 | 0.1 | 0.4 |
| 58 | Filipendula vulgaris | 0 | 0.1 | 0.1 | 0.2 | 0 | 0.4 | 0.1 | 0.3 | 0 | 0.2 | 0.1 | 0.3 | 0 | 0 | 0 | 0 |
| 59 | Frangula alnus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 60 | Galium | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0.8 | 0 | 0.1 | 0.1 | 0.3 | 0 | 0.1 | 0 | 0.3 |
| 61 | Geranium | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0.6 | 0 | 0 | 0.1 | 0 | 0.1 | 0 | 0 |
| 62 | Geranium robertianum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 63 | Geum | 0 | 0.8 | 0.2 | 2 | 0 | 0 | 0 | 1.4 | 0 | 0.2 | 0 | 1.2 | 0 | 0.4 | 0 | 0.6 |
| 64 | Glyceria | 0 | 0.1 | 0.2 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0.1 | 0.2 | 0.2 |
| 65 | Glycine max | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 66 | Gnaphalieae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 67 | Gypsophila | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 68 | Hedera helix | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 69 | Helianthemum nummularium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| 70 | Heuchera richardsonii | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 71 | Hippocastanoideae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 72 | Hippophae rhamnoides | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 73 | Holcus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 74 | Hordeum | 0 | 0 | 0.1 | 0 | 0 | 0.2 | 0.3 | 0 | 0 | 0.2 | 0.6 | 0.3 | 0 | 0.1 | 0.1 | 0.2 |
| 75 | Hottonia palustris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 76 | Hylotelephium telephium | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 77 | Hypericum | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 |
| 78 | Hypnales | 0 | 0.1 | 0.1 | 0.1 | 0 | 0.1 | 0.9 | 0 | 0.3 | 0.1 | 0.2 | 0 | 0 | 0.4 | 0 | 0.1 |
| 79 | Iris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 |
| 80 | Juglans regia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 81 | Juncus | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 82 | Juncus ranarius | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 83 | Juniperus | 4.1 | 0 | 0.2 | 0.1 | 3.9 | 0.5 | 0.1 | 0.2 | 0.6 | 0 | 0 | 0 | 2.5 | 0.4 | 0.8 | 0 |
| 84 | Lamiales | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0.1 |
| 85 | Lathraea squamaria | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 86 | Lathyrus | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 87 | Lathyrus pratensis | 0 | 0 | 0.6 | 2.6 | 0 | 0 | 0.3 | 12.2 | 0 | 0 | 0.6 | 6 | 0 | 0 | 0.2 | 1.2 |
| 88 | Leontodon hispidus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 89 | Ligustrum vulgare | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 90 | Limosella aquatica | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 91 | Linnaea borealis | 0 | 0.4 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 |
| 92 | Linum usitatissimum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 93 | Lotus corniculatus | 0 | 0 | 0.7 | 0.7 | 0 | 0.2 | 0 | 1.5 | 0 | 0.6 | 0.1 | 0.9 | 0 | 0 | 0.3 | 0.4 |
| 94 | Lupinus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 |
| 95 | Luzula | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 96 | Luzula pilosa | 0 | 5.5 | 0.9 | 1.1 | 0.1 | 1 | 0.2 | 0 | 0 | 2.9 | 0.3 | 0.2 | 0 | 3.5 | 0.5 | 0.3 |
| 97 | Lycopodioideae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 98 | Lycopus europaeus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 99 | Lysimachia | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0 |
| 100 | Lysimachia thyrsiflora | 0 | 0 | 0 | 0 | 0 | 0.2 | 0.1 | 0.2 | 0 | 0 | 0 | 0.9 | 0 | 0 | 0 | 0 |
| 101 | Lysimachia vulgaris | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 | 0.8 | 0 | 0.3 | 0 | 0.3 | 0 | 0 | 0 | 0 |
| 102 | Lythrum salicaria | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.3 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| 103 | Medicago | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| 104 | Melampyrum pratense | 0 | 0 | 0 | 0 | 0 | 2.1 | 1.3 | 0.5 | 0 | 0.5 | 0.4 | 0.8 | 0 | 0 | 0 | 0 |
| 105 | Melampyrum sylvaticum | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.4 | 0 | 0 | 0.1 | 0.1 | 0.1 | 0 | 0 | 0 | 0 |
| 106 | Mentha | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 107 | Mentheae | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 108 | Menyanthes trifoliata | 0.1 | 0.3 | 0.4 | 0 | 0 | 0.3 | 0.6 | 0 | 0 | 0.1 | 0.6 | 0 | 0 | 0.1 | 0 | 0 |
| 109 | Mesangiospermae | 0 | 0 | 0.1 | 0.2 | 0.1 | 0.2 | 0.1 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 110 | Micranthes nudicaulis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 111 | Myosotis arvensis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 |
| 112 | Myrica gale | 0 | 3.5 | 0.1 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 6.7 | 0.9 | 0 |
| 113 | Nymphaeaceae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 114 | Oenantheae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 115 | Oleeae | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0.1 |
| 116 | Orthilia secunda | 0 | 0.2 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 117 | Oryza sativa | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 118 | Oxalis acetosella | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.3 | 0 | 0.1 | 0 | 0.1 | 0 | 0 |
| 119 | PACMAD clade | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0 |
| 120 | Pentapetalae | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0 |
| 121 | Persicaria | 0 | 0 | 0 | 0 | 0 | 0.9 | 1.5 | 9.4 | 0.1 | 1.3 | 0.9 | 3.4 | 0 | 0 | 0 | 0.4 |
| 122 | Phragmites australis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 123 | Picea | 1.7 | 1.9 | 2.2 | 6.7 | 2.7 | 0.9 | 5.6 | 5.5 | 0.1 | 0.3 | 0.4 | 1 | 2.4 | 2.1 | 1.1 | 5.1 |
| 124 | Pilosella | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 125 | Pinaceae | 0.1 | 0.2 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 |
| 126 | Pinus | 43 | 4.3 | 2.2 | 3.3 | 22.7 | 6.6 | 3.4 | 3.2 | 5.8 | 0.1 | 0.8 | 0.5 | 49.2 | 8.3 | 3.4 | 4 |
| 127 | Pinus contorta | 0.1 | 0 | 0 | 0 | 0.2 | 0.1 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 128 | Piptatheropsis pungens | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 129 | Pisum sativum | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 |
| 130 | Plantago | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0.1 | 0.1 |
| 131 | Plantago lanceolata | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0.1 |
| 132 | Poa | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 133 | Poales | 0 | 0.1 | 0.1 | 0.1 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0.2 |
| 134 | Poeae | 0 | 0.3 | 0.4 | 1.7 | 0 | 0.1 | 0 | 2.7 | 0 | 0.1 | 0.3 | 0.4 | 0 | 0.2 | 0.2 | 0.7 |
| 135 | Poinae | 0.1 | 2.8 | 2.3 | 3.9 | 0.2 | 1.9 | 0.7 | 1 | 0.1 | 1 | 2.4 | 2.5 | 0.1 | 0.3 | 1.3 | 1.4 |
| 136 | Polygonum | 0 | 0 | 0.2 | 0.1 | 0 | 0 | 0.2 | 0.2 | 0 | 0 | 0.1 | 0.9 | 0 | 0 | 0.1 | 0.1 |
| 137 | Polypodiales | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.2 | 0.3 | 0 | 0 | 0 | 0 | 0.1 |
| 138 | Polypodium vulgare | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 139 | Pooideae | 0.1 | 0.2 | 1.2 | 3.5 | 0 | 0 | 0.3 | 1.1 | 0 | 0.1 | 0.8 | 4.3 | 0.2 | 0.1 | 1.3 | 3.9 |
| 140 | Populus | 2.2 | 1 | 1 | 0.7 | 2.3 | 1.3 | 0.4 | 0.3 | 1 | 0.2 | 0.8 | 0.4 | 1 | 0.7 | 0.8 | 1 |
| 141 | Potentilla | 0 | 0 | 0 | 0.3 | 0 | 0.5 | 0 | 1.5 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0.1 |
| 142 | Primula | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 143 | Prunus | 0.1 | 0.2 | 0.2 | 0.2 | 0.4 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.3 | 0.1 | 0.3 | 0 | 0.2 |
| 144 | Pteridium aquilinum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 145 | Pyrola | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| 146 | Pyrola rotundifolia | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 147 | Pyrus communis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 148 | Quercus | 0.1 | 0.4 | 0.1 | 0.3 | 0 | 0 | 0.1 | 3.6 | 0.1 | 1.2 | 0.1 | 4.6 | 0.1 | 0.1 | 0 | 0.8 |
| 149 | Ranunculus | 0 | 0.9 | 1.5 | 3.4 | 0 | 0.1 | 0.7 | 0.9 | 0.2 | 0.7 | 0.7 | 2.3 | 0.1 | 0.2 | 1 | 2.3 |
| 150 | Rhinanthus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 151 | Rhododendron | 0.2 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.1 | 0 |
| 152 | Ribes | 0 | 0.1 | 0 | 0.8 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.2 | 0 | 0 |
| 153 | Rosa | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 1.2 | 0 | 0 | 0 | 0.8 | 0 | 0 | 0 | 0 |
| 154 | Rosales | 0.9 | 2.2 | 0.9 | 0.3 | 3.2 | 4.7 | 4.8 | 0.2 | 5.2 | 3.4 | 2.1 | 1.3 | 0.3 | 1.5 | 0.9 | 0.6 |
| 155 | Rosoideae | 0 | 0.6 | 0.1 | 0.6 | 0.2 | 9.5 | 0.9 | 0.8 | 0.5 | 4.3 | 0.3 | 1.4 | 0.2 | 0.2 | 0 | 0.1 |
| 156 | Rubieae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 157 | Rubus | 0.2 | 0.3 | 0.3 | 0.9 | 0.3 | 0.2 | 3 | 4.7 | 2.8 | 13.3 | 3 | 10.7 | 1 | 0.4 | 0.1 | 0.6 |
| 158 | Rumex | 0 | 0.4 | 0.5 | 2.7 | 0 | 2.5 | 0.8 | 0.6 | 0 | 3.1 | 1.5 | 1.3 | 0 | 0.3 | 0.2 | 0.8 |
| 159 | Saliceae | 2.7 | 1.2 | 1 | 0.8 | 5.7 | 4.4 | 4.5 | 1.8 | 9.5 | 1.9 | 6.1 | 3.4 | 1.9 | 1.2 | 1.1 | 0.6 |
| 160 | Salix triandra | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 161 | Sambucus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 162 | Sanguisorba officinalis | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 163 | Sarracenia purpurea | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 164 | Saxifraga | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 165 | Saxifraga granulata | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 166 | Scandicinae | 0 | 0.1 | 0 | 0.1 | 0 | 0.1 | 0 | 0.1 | 0 | 0.4 | 0 | 0.1 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 167 | Scirpus | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 168 | Sciuro-hypnum | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 169 | Scorzoneroides autumnalis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 170 | Securigera varia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 |
| 171 | Sedum album | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 172 | Sedum sexangulare | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 173 | Selineae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| 174 | Senecioninae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 175 | Silene | 0 | 0.1 | 0.1 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 176 | Solanoideae | 0.1 | 0.2 | 0.1 | 0.1 | 0.4 | 0 | 0.1 | 0 | 0.1 | 0 | 0.2 | 0.2 | 0 | 0 | 0.1 | 0 |
| 177 | Sparganium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.4 | 0.2 | 0 | 0 | 0 | 0 |
| 178 | Spergula arvensis | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.9 | 0 | 0 | 0 | 0 | 0.1 |
| 179 | Spergularia rubra | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 180 | Sphagnum russowii | 0 | 0 | 0.1 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0.2 | 0.9 | 0.7 | 0 | 0 | 0 | 0 |
| 181 | Spiraea | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 |
| 182 | Splachnum vasculosum | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 183 | Stellaria | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| 184 | Stellaria pallida | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0.3 |
| 185 | Stipeae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 186 | Tetraplodon pallidus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 187 | Trientalis | 0 | 0 | 0 | 0 | 0 | 0.9 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 |
| 188 | Trifolium | 0.4 | 1.7 | 5.6 | 7.3 | 0.1 | 0.1 | 1.9 | 4.1 | 0.1 | 3.9 | 3.3 | 3.3 | 1.2 | 2.8 | 9.6 | 12.7 |
| 189 | Trifolium michelianum | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.2 |
| 190 | Tripleurospermum maritimum | 0 | 0.1 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0.1 | 0 | 0.1 |
| 191 | Triticeae | 0.2 | 0.5 | 1.2 | 1.8 | 0.1 | 0.1 | 0.7 | 0.4 | 0.1 | 0.1 | 0.6 | 0.8 | 0.2 | 0.4 | 0.8 | 1.3 |
| 192 | Typha | 0 | 0 | 0.3 | 0.3 | 0.1 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| 193 | Ulmus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 194 | Urtica | 0 | 0.1 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0.1 | 0 | 0 |
| 195 | Vaccinium | 22 | 28.3 | 15.5 | 16.4 | 30.5 | 13.7 | 6 | 11.5 | 24.7 | 7 | 3.2 | 2 | 18.7 | 30.4 | 20.8 | 19 |
| 196 | Vaccinium microcarpum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 197 | Vaccinium ovalifolium | 12.2 | 15.7 | 8.6 | 9.3 | 17.1 | 8.1 | 3.3 | 6.2 | 12.7 | 3.5 | 1.6 | 1 | 10.1 | 16.2 | 11.3 | 10.3 |
| 198 | Vaccinium oxycoccos | 0 | 0.3 | 0.2 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0.4 | 0.1 | 0.6 |
| 199 | Vaccinium uliginosum | 0 | 0 | 0 | 0.3 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 200 | Vaccinium vitis-idaea | 0.8 | 7.4 | 27.3 | 6.7 | 0.4 | 2 | 5.6 | 0.1 | 1.4 | 10.1 | 15.4 | 3.1 | 1.3 | 4.9 | 19.5 | 5 |
| 201 | Veronica chamaedrys | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 |
| 202 | Veronica officinalis | 0 | 0.1 | 0.1 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0.1 | 0 | 0.2 |
| 203 | Veronica serpyllifolia | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 |

| MOTU No. | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 204 | Vicia | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0.5 | 0 | 0 | 0.1 | 0.7 | 0 | 0 | 0 | 0 |
| 205 | Vicia faba | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.2 | 0.1 | 0 | 0 | 0 |
| 206 | Vinca minor | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 207 | Viola | 0 | 0 | 0 | 0.1 | 0 | 0.3 | 0 | 0 | 0 | 0.2 | 0 | 0.1 | 0 | 0 | 0 | 0 |

Appendix 2c. *Frequency of occurrence (FOO) for 207 MOTUs in Swedish deer diets (Aa: moose, Cc: roe deer, Ce: red deer, and Dd: fallow deer) in different seasons. FOO is stated as the percentage of samples in which a MOTU was detected. The detection threshold was set to ≥ 1%, i.e., in order to be counted a MOTU had to represent at least 1% of the DNA reads in a sample. The sample size (number of faecal samples for each deer species) is given in parentheses.*

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Aa (556) | Cc (143) | Ce (316) | Dd (223) | Aa (169) | Cc (15) | Ce (70) | Dd (22) | Aa (131) | Cc (35) | Ce (97) | Dd (48) | Aa (216) | Cc (135) | Ce (182) | Dd (200) |
| 1 | Abies | 2.9 | 2.8 | 4.4 | 6.3 | 1.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.4 | 2.2 | 0.5 | 0.5 |
| 2 | Acer | 0.7 | 2.1 | 0.6 | 4.9 | 0.6 | 0 | 4.3 | 27.3 | 1.5 | 8.6 | 3.1 | 6.3 | 0.9 | 4.4 | 0 | 8 |
| 3 | Achillea millefolium | 0.9 | 3.5 | 13.3 | 26 | 0 | 6.7 | 2.9 | 27.3 | 0 | 14.3 | 3.1 | 27.1 | 1.9 | 4.4 | 15.4 | 34 |
| 4 | Aegopodium | 0.2 | 3.5 | 0 | 6.3 | 0 | 0 | 0 | 4.5 | 0 | 0 | 2.1 | 6.3 | 0 | 1.5 | 0 | 1 |
| 5 | Agrimonia eupatoria | 0 | 0 | 0 | 3.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 |
| 6 | Agrostidinae | 1.8 | 14.7 | 24.4 | 52.9 | 2.4 | 6.7 | 17.1 | 31.8 | 3.1 | 20 | 14.4 | 50 | 0.5 | 5.9 | 17 | 42 |
| 7 | Alchemilla | 0.5 | 1.4 | 1.6 | 4.9 | 0 | 0 | 0 | 9.1 | 3.8 | 0 | 1 | 0 | 0 | 0.7 | 1.6 | 0 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 8 | Alnus | 44.4 | 43.4 | 21.8 | 24.2 | 38.5 | 40 | 24.3 | 81.8 | 83.2 | 40 | 36.1 | 72.9 | 48.1 | 52.6 | 35.2 | 45 |
| 9 | Alnus alnobetula | 0.5 | 0.7 | 0.3 | 0 | 1.2 | 6.7 | 0 | 0 | 1.5 | 0 | 2.1 | 14.6 | 0.5 | 0 | 0.5 | 1 |
| 10 | Alopecurus geniculatus | 0.4 | 2.8 | 11.1 | 1.3 | 0 | 0 | 10 | 0 | 0.8 | 2.9 | 11.3 | 8.3 | 0.5 | 3 | 4.9 | 3.5 |
| 11 | Andromeda polifolia | 0.2 | 6.3 | 1.6 | 5.4 | 0 | 33.3 | 2.9 | 0 | 0 | 2.9 | 1 | 2.1 | 0 | 5.2 | 2.7 | 2.5 |
| 12 | Anemone | 0.2 | 10.5 | 3.2 | 11.2 | 0 | 0 | 0 | 4.5 | 0 | 0 | 1 | 8.3 | 0 | 0 | 0 | 1.5 |
| 13 | Anthemideae | 0.7 | 4.2 | 10.4 | 15.2 | 0 | 0 | 4.3 | 31.8 | 0.8 | 17.1 | 1 | 14.6 | 0 | 3 | 14.3 | 18 |
| 14 | Apioideae | 1.1 | 0.7 | 2.8 | 1.8 | 3.6 | 0 | 0 | 0 | 4.6 | 2.9 | 3.1 | 4.2 | 1.4 | 0 | 1.1 | 1.5 |
| 15 | Arabis alpina | 0.2 | 2.1 | 1.3 | 0 | 1.8 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1.4 | 0.7 | 0.5 | 0 |
| 16 | Arctostaphylos uva-ursi | 0 | 5.6 | 2.5 | 0.4 | 0 | 20 | 1.4 | 0 | 0 | 17.1 | 1 | 0 | 0 | 6.7 | 7.7 | 0.5 |
| 17 | Asteraceae | 4.5 | 19.6 | 25.6 | 46.6 | 5.3 | 6.7 | 17.1 | 68.2 | 12.2 | 31.4 | 20.6 | 64.6 | 2.3 | 11.1 | 24.7 | 36 |
| 18 | Asterales | 0 | 0.7 | 0.3 | 0.4 | 1.8 | 0 | 0 | 0 | 2.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | Asteroideae | 0.4 | 10.5 | 5.7 | 8.1 | 0 | 6.7 | 4.3 | 9.1 | 0 | 2.9 | 6.2 | 12.5 | 0 | 5.9 | 4.4 | 7 |
| 20 | Aulacomnium | 0.2 | 0 | 0.6 | 0.4 | 0 | 0 | 1.4 | 0 | 0 | 2.9 | 2.1 | 2.1 | 0 | 0 | 0 | 0 |
| 21 | Avena | 0.2 | 13.3 | 2.5 | 2.2 | 0 | 13.3 | 1.4 | 0 | 2.3 | 0 | 11.3 | 12.5 | 1.9 | 6.7 | 2.7 | 11 |
| 22 | Avenella flexuosa | 3.2 | 21.7 | 43.7 | 37.2 | 0.6 | 13.3 | 52.9 | 22.7 | 20.6 | 20 | 71.1 | 54.2 | 6 | 20.7 | 46.7 | 50.5 |
| 23 | Aveninae | 0.2 | 0 | 0 | 0.4 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 |
| 24 | Beta vulgaris | 0.4 | 2.8 | 0.9 | 0.4 | 0 | 0 | 0 | 0 | 0.8 | 0 | 0 | 0 | 0 | 3 | 0.5 | 2 |
| 25 | Betula | 81.3 | 51.7 | 46.2 | 41.7 | 70.4 | 93.3 | 84.3 | 90.9 | 96.9 | 94.3 | 91.8 | 89.6 | 81.5 | 60.7 | 65.4 | 60.5 |
| 26 | Betulaceae | 8.6 | 4.2 | 4.1 | 17 | 4.7 | 6.7 | 35.7 | 27.3 | 9.9 | 11.4 | 25.8 | 22.9 | 8.3 | 6.7 | 4.9 | 15 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27 | Bistorta vivipara | 0.2 | 0 | 0 | 0.9 | 0 | 0 | 1.4 | 0 | 0 | 2.9 | 2.1 | 2.1 | 0 | 0 | 1.1 | 0 |
| 28 | Brachytheciaceae | 0.2 | 0.7 | 0 | 3.6 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.1 | 1.5 |
| 29 | Brassica oleracea | 0.5 | 0.7 | 0.3 | 0.4 | 1.8 | 0 | 2.9 | 0 | 0 | 0 | 0 | 4.2 | 0 | 0 | 1.1 | 0.5 |
| 30 | Brassicaceae | 1.1 | 5.6 | 2.2 | 1.8 | 3 | 6.7 | 0 | 0 | 5.3 | 0 | 5.2 | 0 | 0.9 | 6.7 | 0 | 6 |
| 31 | Bryonia dioica | 0.7 | 1.4 | 3.2 | 2.2 | 3 | 0 | 2.9 | 0 | 0 | 0 | 1 | 0 | 0 | 0.7 | 1.6 | 0.5 |
| 32 | Bryum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.9 | 0 | 0 | 0 | 0 | 0 | 0 |
| 33 | Calluna vulgaris | 22.7 | 69.9 | 79.7 | 62.3 | 3 | 26.7 | 18.6 | 13.6 | 4.6 | 25.7 | 38.1 | 56.3 | 22.7 | 68.9 | 94.5 | 78.5 |
| 34 | Cannabis sativa | 0.5 | 0 | 0.3 | 0 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0 | 0 | 0 | 1.5 | 0 | 0.5 |
| 35 | Carduinae | 0.7 | 25.9 | 20.9 | 30.9 | 0.6 | 13.3 | 5.7 | 45.5 | 2.3 | 25.7 | 8.2 | 52.1 | 5.6 | 24.4 | 23.1 | 41.5 |
| 36 | Carex | 0.2 | 2.8 | 7.9 | 4.9 | 0.6 | 6.7 | 1.4 | 0 | 0.8 | 0 | 3.1 | 2.1 | 0 | 2.2 | 7.7 | 4.5 |
| 37 | Carum carvi | 0 | 0 | 0.9 | 1.3 | 0 | 0 | 0 | 4.5 | 0 | 0 | 1 | 0 | 0 | 0 | 0.5 | 2 |
| 38 | Chamaedaphne calyculata | 0.4 | 1.4 | 0.6 | 3.1 | 0 | 6.7 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2.2 | 0 | 1.5 |
| 39 | Chamaenerion angustifolium | 0.9 | 2.1 | 4.4 | 0.4 | 12.4 | 40 | 65.7 | 18.2 | 55.7 | 40 | 54.6 | 20.8 | 0 | 1.5 | 2.2 | 1.5 |
| 40 | Chenopodium | 0.2 | 0 | 0.3 | 0.4 | 0 | 0 | 0 | 9.1 | 0.8 | 2.9 | 1 | 4.2 | 0 | 0 | 0 | 4 |
| 41 | Chenopodium suecicum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6.3 | 0 | 0 | 0 | 1.5 |
| 42 | Cirsium arvense | 0.4 | 4.9 | 3.2 | 13 | 0 | 6.7 | 1.4 | 31.8 | 0 | 5.7 | 2.1 | 14.6 | 3.2 | 8.1 | 5.5 | 17.5 |
| 43 | Comarum palustre | 0.2 | 2.8 | 0.9 | 0 | 3 | 26.7 | 15.7 | 4.5 | 3.1 | 17.1 | 8.2 | 10.4 | 0 | 5.2 | 3.3 | 0 |
| 44 | Cornus suecica | 0 | 0 | 0.3 | 0 | 0 | 40 | 8.6 | 0 | 0.8 | 17.1 | 2.1 | 2.1 | 0 | 0 | 0.5 | 0 |
| 45 | Corydalis solida | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0.5 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 46 | Crepidinae | 0 | 0 | 0.6 | 2.2 | 0.6 | 0 | 1.4 | 0 | 0 | 0 | 3.1 | 6.3 | 0 | 2.2 | 0.5 | 4 |
| 47 | Dactylis glomerata | 0.4 | 2.1 | 1.9 | 20.2 | 0 | 0 | 0 | 22.7 | 0 | 0 | 0 | 4.2 | 0 | 0.7 | 2.7 | 10.5 |
| 48 | Dryopteris | 1.1 | 37.1 | 44.3 | 21.5 | 1.8 | 20 | 15.7 | 22.7 | 3.8 | 8.6 | 16.5 | 22.9 | 2.3 | 31.1 | 35.2 | 32 |
| 49 | Empetrum | 0.9 | 4.2 | 5.1 | 0.4 | 4.1 | 0 | 4.3 | 0 | 1.5 | 0 | 10.3 | 0 | 1.4 | 1.5 | 6.6 | 1 |
| 50 | Epilobium | 0.2 | 0.7 | 3.2 | 3.1 | 0.6 | 0 | 1.4 | 13.6 | 3.1 | 11.4 | 7.2 | 16.7 | 0 | 3.7 | 1.1 | 1.5 |
| 51 | Ericaceae | 0 | 8.4 | 1.6 | 2.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.2 | 0 | 4.4 | 1.1 | 1.5 |
| 52 | Eriophorum | 0 | 2.8 | 7 | 3.6 | 1.2 | 6.7 | 0 | 0 | 0.8 | 0 | 3.1 | 0 | 0 | 0 | 1.6 | 2 |
| 53 | Eudicotyledons | 0.4 | 0 | 0.6 | 0 | 1.2 | 0 | 1.4 | 0 | 0 | 2.9 | 0 | 2.1 | 0.5 | 0 | 1.1 | 0 |
| 54 | Euphorbia palustris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.7 | 0 | 0 |
| 55 | Fagus sylvatica | 0 | 0 | 0.6 | 0 | 0.6 | 0 | 0 | 0 | 0 | 0 | 1 | 2.1 | 0 | 0 | 0 | 0 |
| 56 | Fallopia | 0.2 | 0 | 0.3 | 0 | 0 | 0 | 4.3 | 0 | 0 | 2.9 | 3.1 | 10.4 | 0 | 1.5 | 0 | 3.5 |
| 57 | Filipendula ulmaria | 0.9 | 17.5 | 13.9 | 23.3 | 7.1 | 26.7 | 24.3 | 81.8 | 8.4 | 48.6 | 9.3 | 45.8 | 1.9 | 10.4 | 5.5 | 11.5 |
| 58 | Filipendula vulgaris | 0.2 | 9.1 | 2.8 | 11.2 | 1.2 | 20 | 12.9 | 54.5 | 1.5 | 20 | 4.1 | 25 | 0.9 | 1.5 | 0 | 2 |
| 59 | Frangula alnus | 0.7 | 0.7 | 0 | 0 | 0 | 0 | 1.4 | 4.5 | 3.8 | 0 | 1 | 4.2 | 0.9 | 1.5 | 0 | 1.5 |
| 60 | Galium | 0.5 | 4.2 | 6 | 14.8 | 0.6 | 6.7 | 7.1 | 54.5 | 0 | 5.7 | 5.2 | 37.5 | 0 | 4.4 | 3.8 | 18.5 |
| 61 | Geranium | 1.1 | 1.4 | 3.2 | 4.5 | 5.9 | 0 | 7.1 | 18.2 | 18.3 | 11.4 | 2.1 | 10.4 | 0.9 | 3 | 0.5 | 1 |
| 62 | Geranium robertianum | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.1 | 0 | 1.5 | 0 | 1.5 |
| 63 | Geum | 0.4 | 23.8 | 8.9 | 40.8 | 0 | 0 | 4.3 | 63.6 | 0 | 11.4 | 2.1 | 39.6 | 0 | 15.6 | 3.3 | 28.5 |
| 64 | Glyceria | 0.5 | 4.9 | 4.7 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 3.1 | 12.5 | 0.5 | 7.4 | 10.4 | 13.5 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 65 | Glycine max | 0.4 | 2.1 | 1.9 | 1.3 | 1.8 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0.9 | 0.7 | 1.1 | 0.5 |
| 66 | Gnaphalieae | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 67 | Gypsophila | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 68 | Hedera helix | 0 | 0 | 0 | 0.4 | 0.6 | 0 | 0 | 0 | 0.8 | 0 | 1 | 0 | 0.5 | 0 | 0.5 | 0 |
| 69 | Helianthemum nummularium | 0.2 | 0 | 0.3 | 1.8 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 2.1 | 0.5 | 0 | 0.5 | 0 |
| 70 | Heuchera richardsonii | 0 | 1.4 | 0 | 1.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 2 |
| 71 | Hippocastanoideae | 1.1 | 0 | 2.5 | 4.5 | 1.8 | 0 | 5.7 | 0 | 3.8 | 2.9 | 6.2 | 12.5 | 2.3 | 0.7 | 3.8 | 2.5 |
| 72 | Hippophae rhamnoides | 0.4 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 |
| 73 | Holcus | 0.2 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0.8 | 0 | 0 | 0 | 0 | 0.7 | 0.5 | 0 |
| 74 | Hordeum | 1.1 | 7 | 7.3 | 6.7 | 0.6 | 6.7 | 14.3 | 0 | 4.6 | 2.9 | 19.6 | 14.6 | 0 | 7.4 | 6 | 8.5 |
| 75 | Hottonia palustris | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 |
| 76 | Hylotelephium telephium | 0 | 0.7 | 0.6 | 1.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.1 | 0 | 0 | 0 | 0 |
| 77 | Hypericum | 0 | 0 | 1.3 | 7.6 | 0 | 0 | 1.4 | 22.7 | 0 | 2.9 | 1 | 2.1 | 0 | 0 | 1.1 | 1.5 |
| 78 | Hypnales | 2.3 | 5.6 | 9.2 | 11.7 | 4.7 | 20 | 7.1 | 0 | 4.6 | 14.3 | 15.5 | 8.3 | 0.5 | 4.4 | 8.2 | 14.5 |
| 79 | Iris | 0 | 1.4 | 0.6 | 0.4 | 0 | 0 | 0 | 4.5 | 0 | 0 | 4.1 | 2.1 | 0 | 0 | 0 | 0.5 |
| 80 | Juglans regia | 0.4 | 0 | 0.6 | 0.4 | 1.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.1 | 0 |
| 81 | Juncus | 0.5 | 0.7 | 3.8 | 3.6 | 0.6 | 0 | 0 | 18.2 | 0 | 2.9 | 2.1 | 6.3 | 0.5 | 0 | 1.6 | 7.5 |
| 82 | Juncus ranarius | 0 | 0 | 0.3 | 0.4 | 0 | 0 | 1.4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 83 | Juniperus | 80.4 | 2.1 | 7 | 9 | 65.1 | 20 | 4.3 | 4.5 | 25.2 | 0 | 2.1 | 6.3 | 67.1 | 18.5 | 14.3 | 5 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 84 | Lamiales | 0.5 | 6.3 | 2.5 | 10.3 | 0.6 | 0 | 2.9 | 50 | 0 | 0 | 1 | 33.3 | 0 | 2.2 | 0.5 | 12.5 |
| 85 | Lathraea squamaria | 0 | 1.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 86 | Lathyrus | 0 | 2.1 | 2.8 | 5.8 | 0 | 0 | 0 | 13.6 | 0 | 0 | 0 | 10.4 | 0 | 0 | 0.5 | 5 |
| 87 | Lathyrus pratensis | 1.3 | 1.4 | 17.4 | 46.6 | 2.4 | 0 | 10 | 95.5 | 4.6 | 11.4 | 18.6 | 79.2 | 2.3 | 3 | 14.8 | 37.5 |
| 88 | Leontodon hispidus | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 |
| 89 | Ligustrum vulgare | 0.2 | 0.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.7 | 0 | 0 |
| 90 | Limosella aquatica | 0.2 | 0 | 0.3 | 0.4 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 91 | Linnaea borealis | 0.7 | 17.5 | 3.8 | 0.9 | 0.6 | 6.7 | 1.4 | 0 | 3.1 | 0 | 2.1 | 2.1 | 0 | 11.9 | 3.8 | 1 |
| 92 | Linum usitatissimum | 0.2 | 0 | 0.6 | 0 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 |
| 93 | Lotus corniculatus | 1.1 | 0.7 | 7.6 | 12.6 | 0.6 | 6.7 | 1.4 | 50 | 0.8 | 2.9 | 8.2 | 37.5 | 2.8 | 0 | 6.6 | 13.5 |
| 94 | Lupinus | 0 | 0 | 0 | 1.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.4 | 0 | 4 |
| 95 | Luzula | 0.5 | 1.4 | 0.3 | 3.1 | 0 | 6.7 | 0 | 9.1 | 0 | 2.9 | 0 | 0 | 0 | 3 | 1.6 | 3 |
| 96 | Luzula pilosa | 4 | 57.3 | 35.4 | 40.8 | 4.7 | 20 | 10 | 4.5 | 3.1 | 28.6 | 22.7 | 20.8 | 0 | 40 | 20.9 | 30 |
| 97 | Lycopodioideae | 0 | 0 | 0.3 | 0 | 0 | 0 | 1.4 | 0 | 0 | 0 | 2.1 | 0 | 0 | 0.7 | 0.5 | 0.5 |
| 98 | Lycopus europaeus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 99 | Lysimachia | 0.2 | 3.5 | 0.3 | 4.9 | 0 | 0 | 0 | 9.1 | 0 | 0 | 0 | 2.1 | 0 | 1.5 | 0 | 2 |
| 100 | Lysimachia thyrsiflora | 0.2 | 1.4 | 1.6 | 0.4 | 0.6 | 6.7 | 14.3 | 27.3 | 2.3 | 5.7 | 6.2 | 16.7 | 0 | 0 | 1.6 | 0.5 |
| 101 | Lysimachia vulgaris | 0 | 0 | 0.6 | 3.6 | 0 | 13.3 | 7.1 | 40.9 | 0.8 | 2.9 | 2.1 | 14.6 | 0 | 1.5 | 0 | 1 |
| 102 | Lythrum salicaria | 0 | 0.7 | 0 | 0 | 0 | 6.7 | 4.3 | 4.5 | 0 | 2.9 | 2.1 | 10.4 | 0 | 0.7 | 0 | 0 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 103 | Medicago | 0.9 | 1.4 | 1.6 | 2.2 | 0 | 0 | 0 | 0 | 0.8 | 2.9 | 4.1 | 6.3 | 0.5 | 0.7 | 2.2 | 3.5 |
| 104 | Melampyrum pratense | 1.3 | 0 | 2.8 | 2.2 | 3 | 40 | 35.7 | 31.8 | 3.1 | 11.4 | 17.5 | 25 | 0.5 | 1.5 | 2.2 | 3 |
| 105 | Melampyrum sylvaticum | 0.2 | 2.8 | 2.8 | 0.4 | 0.6 | 20 | 24.3 | 0 | 2.3 | 5.7 | 10.3 | 6.3 | 0.5 | 2.2 | 4.4 | 1 |
| 106 | Mentha | 0 | 0 | 1.9 | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2.2 | 0.5 | 1.5 |
| 107 | Mentheae | 0 | 2.8 | 1.9 | 9 | 0.6 | 0 | 2.9 | 4.5 | 0 | 0 | 0 | 4.2 | 0 | 1.5 | 3.8 | 15 |
| 108 | Menyanthes trifoliata | 1.4 | 4.2 | 8.2 | 0.4 | 1.8 | 20 | 14.3 | 0 | 4.6 | 5.7 | 4.1 | 6.3 | 0 | 3.7 | 0.5 | 0 |
| 109 | Mesangiospermae | 2.2 | 7.7 | 4.7 | 6.3 | 8.3 | 13.3 | 7.1 | 9.1 | 6.9 | 0 | 10.3 | 12.5 | 2.8 | 8.9 | 2.2 | 3.5 |
| 110 | Micranthes nudicaulis | 0 | 1.4 | 0.6 | 0 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 111 | Myosotis arvensis | 0 | 2.8 | 0.9 | 1.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.7 | 1.1 | 2.5 |
| 112 | Myrica gale | 2.5 | 29.4 | 2.2 | 0 | 0.6 | 20 | 1.4 | 0 | 2.3 | 5.7 | 2.1 | 0 | 0.9 | 40.7 | 12.6 | 0 |
| 113 | Nymphaeaceae | 0.2 | 0 | 0.3 | 0.4 | 0.6 | 0 | 2.9 | 0 | 0 | 0 | 1 | 0 | 0 | 0.7 | 1.1 | 0 |
| 114 | Oenantheae | 0.2 | 0.7 | 0.6 | 0 | 0 | 0 | 1.4 | 0 | 0 | 0 | 4.1 | 0 | 0 | 0 | 1.6 | 0 |
| 115 | Oleeae | 1.4 | 3.5 | 1.6 | 6.7 | 0.6 | 6.7 | 0 | 4.5 | 2.3 | 0 | 2.1 | 2.1 | 1.4 | 4.4 | 1.1 | 5 |
| 116 | Orthilia secunda | 0 | 13.3 | 3.2 | 2.2 | 0 | 20 | 1.4 | 0 | 0 | 2.9 | 1 | 2.1 | 0 | 5.2 | 1.6 | 1.5 |
| 117 | Oryza sativa | 0 | 0 | 0.3 | 0.4 | 0 | 0 | 0 | 0 | 0 | 2.9 | 0 | 0 | 0 | 0 | 0.5 | 0.5 |
| 118 | Oxalis acetosella | 0.2 | 10.5 | 2.2 | 3.1 | 0 | 6.7 | 1.4 | 4.5 | 0 | 20 | 2.1 | 14.6 | 0 | 4.4 | 1.6 | 2.5 |
| 119 | PACMAD clade | 0.9 | 2.1 | 1.9 | 1.8 | 0.6 | 0 | 0 | 0 | 1.5 | 0 | 3.1 | 2.1 | 1.4 | 3.7 | 1.1 | 2.5 |
| 120 | Pentapetalae | 2.2 | 3.5 | 5.7 | 5.4 | 2.4 | 6.7 | 5.7 | 0 | 3.8 | 0 | 5.2 | 8.3 | 4.6 | 0.7 | 3.8 | 5 |
| 121 | Persicaria | 0.5 | 0 | 6.3 | 2.2 | 0 | 13.3 | 12.9 | 31.8 | 3.8 | 22.9 | 19.6 | 29.2 | 0 | 0.7 | 2.2 | 10 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 122 | Phragmites australis | 0 | 0 | 1.3 | 0.4 | 0 | 0 | 0 | 9.1 | 0 | 0 | 3.1 | 2.1 | 0.5 | 1.5 | 1.1 | 2 |
| 123 | Picea | 31.5 | 49.7 | 60.8 | 81.6 | 31.4 | 40 | 32.9 | 50 | 10.7 | 42.9 | 28.9 | 33.3 | 39.4 | 40.7 | 58.8 | 83.5 |
| 124 | Pilosella | 0.2 | 1.4 | 0 | 4.9 | 0.6 | 0 | 1.4 | 4.5 | 0 | 0 | 0 | 2.1 | 0 | 0 | 1.1 | 9 |
| 125 | Pinaceae | 1.4 | 1.4 | 2.2 | 1.8 | 3 | 0 | 1.4 | 4.5 | 2.3 | 0 | 4.1 | 2.1 | 1.9 | 1.5 | 1.1 | 1 |
| 126 | Pinus | 97.3 | 58.7 | 66.8 | 80.3 | 80.5 | 40 | 44.3 | 59.1 | 42.7 | 22.9 | 55.7 | 35.4 | 99.5 | 69.6 | 85.7 | 86 |
| 127 | Pinus contorta | 3.6 | 0 | 0.9 | 0.4 | 5.9 | 6.7 | 1.4 | 4.5 | 1.5 | 0 | 1 | 0 | 3.2 | 0 | 1.1 | 0 |
| 128 | Piptatheropsis pungens | 0 | 0 | 0.3 | 0 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 |
| 129 | Pisum sativum | 0.7 | 4.2 | 1.3 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.1 | 0 | 5.2 | 1.1 | 1 |
| 130 | Plantago | 0.4 | 1.4 | 3.5 | 3.1 | 0 | 6.7 | 0 | 9.1 | 0 | 0 | 1 | 14.6 | 0 | 0 | 4.9 | 7.5 |
| 131 | Plantago lanceolata | 0.4 | 1.4 | 1.3 | 7.6 | 0 | 6.7 | 0 | 13.6 | 0 | 0 | 5.2 | 4.2 | 0 | 1.5 | 1.6 | 8 |
| 132 | Poa | 0.4 | 2.8 | 2.5 | 7.6 | 0 | 0 | 2.9 | 4.5 | 3.1 | 0 | 8.2 | 12.5 | 0 | 3 | 2.7 | 5.5 |
| 133 | Poales | 1.3 | 3.5 | 8.5 | 13.5 | 0 | 20 | 5.7 | 9.1 | 0.8 | 0 | 4.1 | 14.6 | 0.9 | 0.7 | 5.5 | 15 |
| 134 | Poeae | 2.7 | 23.1 | 32.3 | 60.5 | 1.2 | 13.3 | 8.6 | 54.5 | 6.1 | 25.7 | 18.6 | 45.8 | 2.8 | 15.6 | 28.6 | 56.5 |
| 135 | Poinae | 5.4 | 39.2 | 58.9 | 68.6 | 3.6 | 6.7 | 20 | 63.6 | 9.9 | 28.6 | 39.2 | 56.3 | 12 | 18.5 | 45.6 | 70 |
| 136 | Polygonum | 0.5 | 2.1 | 4.4 | 4.9 | 0 | 0 | 10 | 22.7 | 0 | 0 | 16.5 | 16.7 | 0.5 | 0.7 | 6.6 | 7 |
| 137 | Polypodiales | 0 | 2.8 | 4.1 | 3.1 | 3 | 0 | 1.4 | 13.6 | 3.1 | 5.7 | 8.2 | 4.2 | 0.5 | 2.2 | 2.2 | 3.5 |
| 138 | Polypodium vulgare | 0.4 | 5.6 | 2.5 | 2.2 | 0 | 0 | 1.4 | 0 | 0 | 2.9 | 1 | 0 | 0.5 | 5.9 | 2.2 | 3.5 |
| 139 | Pooideae | 7.4 | 26.6 | 53.8 | 78.5 | 5.3 | 6.7 | 10 | 59.1 | 6.9 | 5.7 | 29.9 | 68.8 | 8.3 | 20 | 40.1 | 88.5 |
| 140 | Populus | 48.2 | 43.4 | 33.9 | 31.8 | 47.3 | 46.7 | 38.6 | 45.5 | 56.5 | 25.7 | 44.3 | 47.9 | 37.5 | 40 | 32.4 | 32 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 141 | Potentilla | 0.4 | 4.2 | 3.8 | 17 | 1.2 | 33.3 | 8.6 | 72.7 | 0.8 | 5.7 | 3.1 | 52.1 | 0 | 1.5 | 2.7 | 13.5 |
| 142 | Primula | 0 | 0.7 | 0.6 | 5.4 | 0 | 0 | 0 | 4.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 |
| 143 | Prunus | 7.6 | 11.2 | 5.7 | 11.7 | 13.6 | 6.7 | 8.6 | 22.7 | 10.7 | 8.6 | 5.2 | 10.4 | 5.1 | 7.4 | 6 | 7.5 |
| 144 | Pteridium aquilinum | 0 | 0 | 0 | 3.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6.3 | 0 | 0 | 1.6 | 6 |
| 145 | Pyrola | 0 | 2.1 | 1.6 | 1.8 | 0 | 0 | 0 | 0 | 0 | 2.9 | 0 | 2.1 | 0 | 0.7 | 1.1 | 0 |
| 146 | Pyrola rotundifolia | 0 | 3.5 | 0.3 | 0.9 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 147 | Pyrus communis | 0 | 1.4 | 0.3 | 0.4 | 0 | 0 | 0 | 0 | 0.8 | 0 | 0 | 2.1 | 0.5 | 0 | 0 | 2.5 |
| 148 | Quercus | 9.7 | 14.7 | 3.8 | 14.8 | 1.8 | 6.7 | 4.3 | 40.9 | 6.1 | 11.4 | 7.2 | 45.8 | 6 | 10.4 | 3.3 | 19 |
| 149 | Ranunculus | 3.2 | 32.2 | 43 | 69.1 | 2.4 | 6.7 | 12.9 | 72.7 | 9.9 | 34.3 | 29.9 | 66.7 | 4.2 | 21.5 | 42.9 | 68.5 |
| 150 | Rhinanthus | 0 | 0 | 1.9 | 0 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 151 | Rhododendron | 9.2 | 0.7 | 2.5 | 0.9 | 2.4 | 6.7 | 0 | 0 | 0.8 | 0 | 0 | 2.1 | 10.6 | 0 | 3.8 | 0 |
| 152 | Ribes | 1.3 | 8.4 | 0.6 | 9.9 | 0.6 | 0 | 2.9 | 0 | 0.8 | 2.9 | 1 | 2.1 | 1.9 | 10.4 | 0.5 | 0.5 |
| 153 | Rosa | 0.2 | 0.7 | 1.6 | 4 | 0 | 0 | 0 | 40.9 | 0 | 5.7 | 0 | 29.2 | 0.9 | 2.2 | 1.1 | 2.5 |
| 154 | Rosales | 38.1 | 50.3 | 19.9 | 15.7 | 65.7 | 86.7 | 62.9 | 31.8 | 76.3 | 48.6 | 49.5 | 45.8 | 21.3 | 52.6 | 26.4 | 15.5 |
| 155 | Rosoideae | 4.9 | 34.3 | 12 | 41.3 | 8.9 | 46.7 | 54.3 | 81.8 | 48.1 | 77.1 | 34 | 83.3 | 6 | 12.6 | 6 | 24 |
| 156 | Rubieae | 0.2 | 0.7 | 0.9 | 3.1 | 0 | 0 | 0 | 4.5 | 0 | 0 | 0 | 2.1 | 0 | 0 | 0.5 | 4.5 |
| 157 | Rubus | 6.8 | 30.1 | 16.5 | 22 | 16 | 40 | 54.3 | 86.4 | 72.5 | 85.7 | 42.3 | 70.8 | 10.6 | 17 | 9.9 | 16.5 |
| 158 | Rumex | 1.8 | 20.3 | 31.6 | 52.5 | 2.4 | 46.7 | 40 | 59.1 | 10.7 | 57.1 | 44.3 | 50 | 3.7 | 9.6 | 27.5 | 33.5 |
| 159 | Saliceae | 50.7 | 39.9 | 29.7 | 23.3 | 68.6 | 86.7 | 71.4 | 50 | 93.1 | 65.7 | 71.1 | 62.5 | 45.4 | 32.6 | 29.1 | 19 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 160 | Salix triandra | 0.5 | 0 | 0 | 0 | 0.6 | 0 | 0 | 0 | 4.6 | 0 | 0 | 0 | 1.4 | 0.7 | 0 | 0 |
| 161 | Sambucus | 0.4 | 2.1 | 0.6 | 1.8 | 0 | 0 | 2.9 | 0 | 0.8 | 2.9 | 0 | 0 | 0.5 | 5.2 | 0.5 | 1 |
| 162 | Sanguisorba officinalis | 1.6 | 0.7 | 2.2 | 2.7 | 1.2 | 6.7 | 4.3 | 9.1 | 0.8 | 0 | 1 | 4.2 | 1.4 | 0.7 | 1.6 | 3 |
| 163 | Sarracenia purpurea | 1.1 | 0 | 0.3 | 2.2 | 3 | 0 | 0 | 0 | 0.8 | 0 | 0 | 2.1 | 1.4 | 0.7 | 0.5 | 1.5 |
| 164 | Saxifraga | 0 | 0.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 165 | Saxifraga granulata | 0 | 4.9 | 0.3 | 5.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| 166 | Scandicinae | 0.4 | 10.5 | 2.2 | 11.2 | 0.6 | 6.7 | 0 | 22.7 | 5.3 | 22.9 | 2.1 | 18.8 | 0.5 | 1.5 | 0.5 | 5 |
| 167 | Scirpus | 0.2 | 0.7 | 12 | 14.3 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0 | 6.3 | 0 | 0.7 | 0.5 | 2.5 |
| 168 | Sciuro-hypnum | 0.5 | 0.7 | 2.5 | 3.1 | 0 | 6.7 | 2.9 | 0 | 0 | 5.7 | 1 | 0 | 0 | 0 | 0 | 0 |
| 169 | Scorzoneroides autumnalis | 0 | 0.7 | 2.8 | 8.5 | 0 | 0 | 4.3 | 40.9 | 0 | 8.6 | 8.2 | 10.4 | 0 | 1.5 | 1.6 | 7 |
| 170 | Securigera varia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.7 | 0 | 0 |
| 171 | Sedum album | 0 | 1.4 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 172 | Sedum sexangulare | 0 | 1.4 | 0 | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 173 | Selineae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.9 | 0 | 0 | 0 | 0 | 0 | 0.5 |
| 174 | Senecioninae | 0.2 | 0.7 | 0.6 | 1.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.1 | 0 | 0 | 1.1 | 0 |
| 175 | Silene | 0 | 4.2 | 3.5 | 0 | 0 | 13.3 | 2.9 | 0 | 0.8 | 2.9 | 2.1 | 0 | 0 | 1.5 | 0.5 | 0 |
| 176 | Solanoideae | 5.6 | 9.8 | 13 | 13 | 20.7 | 0 | 12.9 | 9.1 | 11.5 | 5.7 | 24.7 | 14.6 | 5.1 | 5.2 | 10.4 | 8.5 |
| 177 | Sparganium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.9 | 1 | 6.3 | 0 | 0 | 0 | 0.5 |
| 178 | Spergula arvensis | 0 | 0 | 0 | 0 | 0 | 0 | 7.1 | 0 | 0 | 2.9 | 9.3 | 8.3 | 0 | 0 | 0 | 0.5 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 179 | Spergularia rubra | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 180 | Sphagnum russowii | 1.3 | 1.4 | 6 | 4 | 0.6 | 6.7 | 4.3 | 4.5 | 10.7 | 22.9 | 27.8 | 12.5 | 1.9 | 5.2 | 3.8 | 2 |
| 181 | Spiraea | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 |
| 182 | Splachnum vasculosum | 0.2 | 0 | 0 | 0 | 0 | 0 | 2.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 183 | Stellaria | 0 | 3.5 | 1.6 | 7.2 | 0 | 0 | 0 | 13.6 | 0.8 | 2.9 | 0 | 0 | 0 | 1.5 | 1.6 | 6.5 |
| 184 | Stellaria pallida | 0 | 0 | 0.3 | 0 | 0 | 0 | 2.9 | 0 | 0 | 2.9 | 5.2 | 0 | 0.5 | 0 | 0 | 1.5 |
| 185 | Stipeae | 0.2 | 0 | 0.6 | 0.4 | 0.6 | 0 | 0 | 0 | 0.8 | 0 | 0 | 2.1 | 0 | 0 | 0 | 0 |
| 186 | Tetraplodon pallidus | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 187 | Trientalis | 0.2 | 0.7 | 2.5 | 0.4 | 0.6 | 33.3 | 20 | 9.1 | 0 | 0 | 9.3 | 4.2 | 0 | 0 | 2.2 | 0 |
| 188 | Trifolium | 9.2 | 29.4 | 58.5 | 70.4 | 4.7 | 20 | 21.4 | 77.3 | 7.6 | 34.3 | 37.1 | 79.2 | 19.4 | 28.9 | 50 | 86.5 |
| 189 | Trifolium michelianum | 0.7 | 2.8 | 11.4 | 13.5 | 0 | 0 | 0 | 13.6 | 0 | 0 | 3.1 | 8.3 | 3.7 | 6.7 | 13.2 | 29.5 |
| 190 | Tripleurospermum maritimum | 0.4 | 7 | 6 | 8.1 | 0 | 6.7 | 0 | 0 | 0 | 0 | 6.2 | 4.2 | 0 | 3 | 3.8 | 6 |
| 191 | Triticeae | 13.3 | 29.4 | 51.3 | 62.8 | 10.7 | 20 | 32.9 | 45.5 | 16.8 | 14.3 | 46.4 | 60.4 | 13.4 | 23.7 | 51.6 | 63.5 |
| 192 | Typha | 1.1 | 0.7 | 3.8 | 3.1 | 3.6 | 6.7 | 5.7 | 4.5 | 0.8 | 0 | 3.1 | 8.3 | 0 | 1.5 | 0 | 1.5 |
| 193 | Ulmus | 0 | 0 | 0.6 | 1.3 | 1.2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0.5 | 0 | 0.5 | 2.5 |
| 194 | Urtica | 0.4 | 5.6 | 1.3 | 1.8 | 0 | 0 | 0 | 0 | 0 | 11.4 | 1 | 0 | 0 | 5.9 | 1.6 | 8 |
| 195 | Vaccinium | 93 | 100 | 97.8 | 93.3 | 97 | 86.7 | 71.4 | 68.2 | 98.5 | 85.7 | 78.4 | 64.6 | 90.3 | 99.3 | 99.5 | 98.5 |
| 196 | Vaccinium microcarpum | 0 | 2.1 | 1.3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.1 | 0 | 1.5 | 0.5 | 3.5 |
| 197 | Vaccinium ovalifolium | 92.1 | 100 | 94.9 | 91.9 | 94.7 | 86.7 | 65.7 | 63.6 | 97.7 | 74.3 | 56.7 | 52.1 | 88.4 | 99.3 | 99.5 | 97 |

| MOTU | Best assignment | Spring | | | | Summer | | | | Autumn | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 198 | Vaccinium oxycoccos | 0.5 | 7 | 8.5 | 9.9 | 0 | 0 | 0 | 0 | 0.8 | 0 | 8.2 | 8.3 | 0 | 4.4 | 5.5 | 12 |
| 199 | Vaccinium uliginosum | 1.6 | 1.4 | 1.3 | 2.7 | 3 | 20 | 1.4 | 13.6 | 2.3 | 2.9 | 4.1 | 2.1 | 1.9 | 0 | 1.6 | 1 |
| 200 | Vaccinium vitis-idaea | 48.4 | 87.4 | 97.5 | 84.3 | 27.8 | 66.7 | 60 | 9.1 | 49.6 | 91.4 | 87.6 | 45.8 | 60.2 | 84.4 | 98.9 | 91.5 |
| 201 | Veronica chamaedrys | 0 | 4.9 | 3.2 | 14.8 | 1.2 | 0 | 1.4 | 9.1 | 0 | 0 | 0 | 8.3 | 0 | 5.2 | 1.1 | 27 |
| 202 | Veronica officinalis | 0.2 | 12.6 | 9.5 | 19.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.2 | 0 | 5.2 | 4.9 | 20 |
| 203 | Veronica serpyllifolia | 0 | 0 | 3.8 | 10.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6.3 | 0.9 | 2.2 | 2.2 | 11 |
| 204 | Vicia | 0.5 | 0.7 | 6.3 | 2.2 | 0.6 | 0 | 12.9 | 54.5 | 4.6 | 5.7 | 17.5 | 39.6 | 0 | 0.7 | 5.5 | 4 |
| 205 | Vicia faba | 0 | 0.7 | 0 | 1.3 | 0 | 0 | 0 | 4.5 | 0 | 2.9 | 1 | 2.1 | 0.5 | 3 | 0 | 2 |
| 206 | Vinca minor | 0 | 2.1 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.2 | 0 | 0.5 |
| 207 | Viola | 0 | 0.7 | 0.3 | 6.7 | 0 | 26.7 | 2.9 | 4.5 | 0 | 17.1 | 3.1 | 16.7 | 0 | 0 | 0 | 0.5 |