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Original article

Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by increased browsing by cervids?

Gunnar Austrheim, Erling J. Solberg & Atle Mysterud

During recent decades, rough livestock grazing has decreased markedly on unimproved land (i.e. natural and semi-natural habitats) across most of Europe, whilst the number of wild cervids has increased. However, we still know little about the overall changes in the herbivore pressure and how herbivore regimes vary between biogeographic regions. We have quantified the spatio-temporal variation in herbivore pressure indirectly by estimating the metabolic biomass of large herbivores in mountain, coastal and inland municipalities of Norway every 10th year during 1949-1999. We quantified how much livestock biomass has decreased, whether this corresponded to increasing cervid biomass, and whether the proportion of grazing relative to browsing has changed within the herbivore community. Total metabolic biomass of livestock and cervids (MBA_{total}) decreased from 126 kg/km^2 in 1949 to 107 kg/km^2 in 1999 (~85% of MBA_{total} in 1949). Changes differed markedly between regions. Herbivore pressure in the coastal region nearly halved from 1949 to 1999, while the decrease was minor in the inland and mountain regions. Livestock grazing more than halved, whereas the metabolic biomass of cervids increased by 276% from 1949 to 1999. Cervids dominated the community of large herbivores on unimproved land in Norway in 1999 (54% of MBA_{total}). Livestock dominated in the mountain (52% of MBA_{total}) and in the coastal region (54% of MBA_{total}) in 1999, while cervids dominated in the inland region (67% of MBA_{total}). Most herbivore foraging consisted of grazing in 1949 (89% at a national scale). This proportion was reduced to 54% by 1999. Percent browsing was especially high (> 90%) in several municipalities in southeastern Norway in 1999. The increase of wild cervids is exceptional in a historical perspective, and managers have to adapt to wild cervids being the major ecosystem engineers in many landscapes.

Key words: biogeographic regions, domestic herbivores, ecosystem management, grazing pressure, herbivory, wild herbivores

Please note that supplementary information including Tables S1- S6, Figures S1-S4 and Appendices SI-SIII mentioned in this article is available in the online version of this article, which can be viewed at www.wildlifebiology.com

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The density and composition of herbivore communities have major impacts on the structure and function of several ecosystems worldwide (Asner et al. 2004). In Europe, as well as in most of the post-industrialised part of the world, the regional distribution of large grazing and browsing herbivores has changed dramatically during the second half of the 20th century (Prins & Gordon 2008). Livestock

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such as cattle *Bos taurus*, horses *Equus caballus*, sheep *Ovis aries* and goats *Capra hircus*, have decreased substantially in numbers (FAO; available at: http://faostat.fao.org/), and changes in husbandry practice (e.g. larger breeds) have led to an increase of grazing in infields (agricultural land) at the expense of rough grazing on unimproved land (i.e. natural and semi-natural habitat) (Dallimer et al. 2009). Free-ranging livestock and wild herbivores are often sympatric, and the decrease in land use by husbandry has at least partly facilitated the large increase in the abundance of wild herbivores in most European countries (Ahlén 1965, 1975). Increased densities and range expansions are evident for most wild herbivores in Europe during the latest decades: especially for moose *Alces alces* in the boreal region of Northern Europe and roe deer *Capreolus capreolus* and red deer *Cervus elaphus* in Europe in general (Apollonio et al. 2010). Even though these patterns are well-known, there are no quantitative studies of the spatial and temporal distribution of livestock and wild herbivores in European unimproved land during the last 50 years.

The regional patterns of large herbivore foraging may vary due to environmental and cultural factors (Milner et al. 2006). In Norway, cervids such as reindeer (semi-domestic and wild) are dominant in the mountain region, moose and roe deer in the more forested inland, whereas red deer are mostly found in the coastal region (Solberg et al. 2003). Although the distributions of livestock differ between regions, there is no obvious regional allocation of livestock species related to their biological requirements. In Europe, livestock are often found in more marginal areas for agricultural production and thus are believed to be more influenced by socio-economic factors (MacDonald et al. 2000, Hadjigeorgiou et al. 2005). The outcome, given as total herbivore pressure of both wild and domestic large herbivores at a more restricted regional scale, is thus an open question.

Large herbivores are managed to meet multiple socio-economic and environmental objectives, and both grazers and browsers are actively used for the conservation of nature reserves (Wallis de Vries et al. 1998, Gordon et al. 2004). Regional variation in grazing and browsing by large herbivores challenges management due to both high and low herbivore pressure. Several examples of overgrazing/-browsing within specific regions have been reported, where herbivores have reached local densities whose sustainability has been questioned (see review in Mysterud 2006). In contrast, low stocking rates and forest succession in former outlying pastures is considered to be a threat to biodiversity for semi-natural habitats, especially in Europe (Zervas 1998, Poschold et al. 2005). Moreover, changes in the spatio-temporal distribution of large herbivores are not just a question of total herbivore pressure. A reduction of livestock (grazers) and an increase of cervid browsers also suggest that the foraging strategy (browsing vs grazing) is changing. In Norway, the strong increase of browsers such as moose and roe deer combined with a decrease in livestock grazers (especially cattle) gives reason to expect a general increase in browsing vs grazing in the non-alpine area, whereas in the coastal and alpine areas, the high abundances of intermediate feeders such as red deer, reindeer and free-grazing sheep is expected to maintain a relative high grazing pressure.

In our study, we examined the spatio-temporal variation in herbivore pressure on unimproved land during the second half of the 20th century in Norway. We measured herbivore pressure indirectly by estimating the metabolic biomass of all large herbivores at the municipality level, as well as the proportion of graze (graminoids and herbs) and browse (woody species) consumed every 10th year from 1949 to 1999. Based on these estimations, we addressed the following questions: 1) What is the relative change in herbivore pressure by domestic, semi-domestic and wild herbivores, and 2) to what extent have changes in herbivore communities affected the relative importance of grazing and browsing? We also asked 3) how the total foraging pressure, the distribution of cervids vs livestock, and the relative importance of grazing and browsing varied on a biogeographic scale? The Norwegian landscape is heterogeneous with strong altitudinal and latitudinal gradients, including three main biomes (temperate and boreal forests, and arctic/alpine tundra) and a strong distinction between coastal and inland areas (Moen 1999). Norway can therefore serve as an interesting case on how temporal variation in foraging pressure and strategies differ between biogeographic regions. Based on this regional perspective, we also emphasise some implications of relevance for local management of large herbivores in heterogeneous landscapes.

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Methods

Study area

Wild herbivores (i.e. reindeer, moose, red deer, roe deer and wild boar *Sus scrofa*) were present in many ecosystems in Norway from early Holocene as documented by palaecological records (Lie 1990, Hufthammer & Aaris-Sørensen 1998, Myhre & Øye 2002, Rosvold et al. 2010). In addition, domestication of reindeer has pre-historic traditions within the Saami reindeer husbandry. Livestock were introduced into Norway 5,000-6,000 BP, and have ever since been an important part of the agricultural economy (Agerskov 2007). Like elsewhere in the boreal region, winters are long and harsh, restricting the amount of fodder for 5-6 months. Exceptions are found in the milder coastal parts, where less demanding breeds of sheep and cattle can forage on unimproved land during mostly snow-free winters. However, the vast majority of livestock is dependent on supplemental food, and accordingly, 60% of the arable land in Norway is used for the production of winter fodder (Agerskov 2007).

The historical importance of livestock farming (Almaas 2004, Austrheim et al. 2008b) depended on herbivores transforming plants from unimproved land into meat, milk, skin and wool. Especially marginal mountainous and coastal areas were used for animal husbandry. In combination with collection of winter-fodder and fuel wood, this farming system shaped the semi-natural subalpine grasslands and coastal heathlands, which today are appreciated as cultural and natural heritages. The economic importance of animal husbandry decreased throughout the 20th century, but unlike most of Europe (Prins & Gordon 2008), the total number of livestock has increased in Norway (Appendix SI). However, following the introduction of artificial fertiliser at the beginning of the 20th century, grazing on unimproved land has declined due to increasing grazing on infields (Austrheim et al. 2008b).

Biogeographic regions of Norway

Data on number and metabolic biomass of large herbivores were sampled at the scale of municipalities (as in 1999), made available by Statistics Norway (available at: http://www.ssb.no/). All municipalities (N = 435) were classified into bio-geographic regions based on climate conditions (oceanity vs continentality) and altitude. A coarse classification includes coastal, inland and mountainous municipalities (Fig.

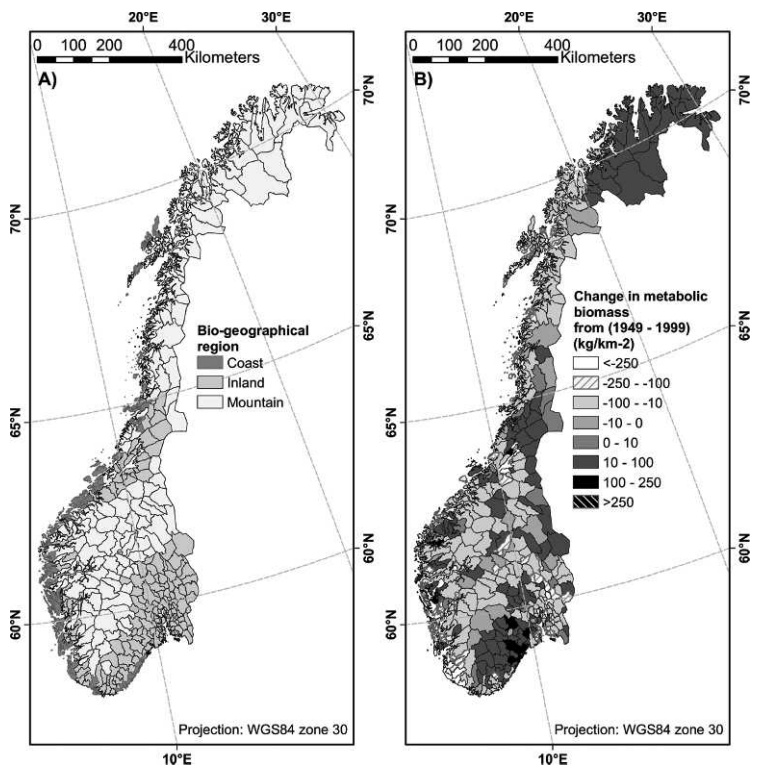


Figure 1. Spatial distribution of the coastal inland and mountain biogeographic regions (A) and the change in metabolic biomass during 1949-1999 (B).

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1). For further details on biogeographic regions see Appendix SI and Table S1.

Livestock number and grazing days on unimproved land

The number of livestock in each municipality was based on surveys conducted every 10th year in June by agricultural authorities and reported to Statistics Norway. In our study, we included data from 1949, 1959, 1969, 1979, 1989 and 1999 (Table S2). Almost all livestock were kept indoors during winter and a large percentage grazed only in infields. Livestock grazing pressure on unimproved land was therefore adjusted in accordance with the number of rough grazing livestock, and the length of the grazing season (Austrheim et al. 2008b). See also Appendix SII.

Cervid numbers

For all cervids, summer densities differ from winter densities due to the autumn harvest. We calculated the annual mean number as:

$$D = ((D_{summer} \times 4) + (D_{winter} \times 8))/12 \qquad (1),$$

where D_{summer} is the density of a given cervid species during summer (four months) while D_{winter} is the density during winter (eight months).

Semi-domestic and wild reindeer

Separate population numbers were estimated for semi-domestic and wild populations. Wild populations are present in southeastern, western and central Norway only. We compiled the number of semi-domestic reindeer from the Norwegian reindeer management authorities (available at: http://www.reindrift.no/), whereas we estimated the numbers of wild reindeer based on aerial surveys (Table S3).

Since most reindeer are migratory (Ims et al. 2007), reindeer numbers were distributed in proportion with the area of unimproved land in all municipalities used by the herd (i.e. same density of reindeer). We used similar procedures to correct for semi-domestic reindeer crossing the Norwegian-Swedish border. For details see Austrheim et al. (2008b).

Moose, red deer and roe deer

To estimate population density of moose, red deer and roe deer, we used a simple population model, which is based on the rationale that the annual number of individuals harvested will equal the number of individuals recruited to the population prior to harvesting (number of new recruits - number of natural mortalities) minus the annual net population growth. Assuming no net migration, the pre-harvest adult (≥1-year old) population size (aN_t) can then be estimated by using the equation:

$$aN_t = Q_t/(R_t - (\lambda - 1)) \qquad (2),$$

where Q is the annual harvest, R is the recruitment rate and λ is the finite population growth rate (N_{t+1}/N_t). We calculated the recruitment rate based on the equation:

$$R_t = (C_t - M)/(1 - C_t) \qquad (3),$$

where C is the pre-harvest proportion calves in the population, and M is the annual natural mortality rate for post-recruitment individuals (i.e. ≥ 4 months; Veiberg et al. 2007, Austrheim et al. 2008b). Likewise, we estimated population growth rate, λ, based on the change in harvest over time, i.e. by regressing the log-annual harvest on year within county (for moose) or country as a whole (for red deer and roe deer). We then calculated λ from the equation $\lambda = e^r$, where r is the regression coefficient (Caughley 1977).

Using these equations, we estimated the pre-harvest adult population (≥1-year old) needed to allow the recorded annual harvest for a given population growth rate. However, as we were interested in the herbivore pressure of the total population, we also included (in the population estimate) the number of individuals that were harvested each year. This represents individuals that are only present in the population for about four months, i.e. from the calving season (around 1 June) to the start of the hunting season (in late September or early October). Accordingly, the average population size, APS_t during the year can be calculated as:

$$APS_t = aN_t + (Q_t \times (4/12)) \qquad (4),$$

where aN_t and Q are as in equation 2 above. We calculated the population density, APD_t, by scaling the population size with the size of the study area, A (in km^2):

$$APD_t = APS_t/A \qquad (5).$$

To parameterise the model, we used natural mortality rates (M) estimated in various studies of moose and deer in Scandinavia, and calf ratios (C) based on the observed proportion of calves in the populations

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during the hunting season. Such observations are regularly recorded by moose and red deer hunting teams all over Norway and are used by local wildlife managers to estimate changes in the population structure (e.g. proportion of calves, calves/female and sex ratios). For roe deer, less is known about the spatio-temporal variation in mortality and recruitment rates, making it more difficult to estimate accurate population densities. For details on population estimation of moose, red deer and roe deer, see Appendix SIII, Table S6 and Figs. S3 and S4.

Estimation of herbivore pressure

We estimated the herbivore pressure indirectly as the metabolic biomass; i.e. the allometric relationship between body weight (BW) and energy requirement ($BW^{0.75}$; Kleiber 1961). We took into account the demographic structure (proportion of males, females and calves) and sex and age-specific weights (Table S4). In addition, we estimated the total number of grazing days for each herbivore at the municipality level. We thus estimated the metabolic biomass (MB) for each municipality and year using the equation:

$$MB = (N_{Female} \times N_D \times BW^{0.75}) + (N_{Male} \times N_D \times BW^{0.75}) + (N_{Calf} \times N_D \times BW^{0.75}) \quad (6),$$

where N_{Female}, N_{Male} and N_{Calf} are the total numbers of animals within a demographic group grazing on unimproved land, N_D is the number of grazing days on unimproved land, and $BW^{0.75}$ is the body weight scaled by the isometric metabolic rate. We calculated the MB/km^2 unimproved land (MBA) by dividing the sum of MB by the area in km^2 (A_o) for all Norwegian municipalities ($MBA = \Sigma MB/\Sigma A_o$). We subtracted non-grazeable land units (i.e. infields, built-over area, lakes and areas permanently covered with snow; provided by Statistics Norway 2003) from the total land area within each municipality to denote the area of unimproved land.

Estimation of grazing vs browsing

We compiled estimates of the relative amount of browsing vs grazing for each herbivore species from the literature (Mysterud 2000), and given for the coast, inland and mountain biogeographic regions if available. Livestock herbivores only forage on unimproved land during summer. For semi-domestic and wild herbivores, at least one recording of diet was available for both summer and winter (Table S5). We used data from a neighbouring region to calculate diet from missing regions. We defined summer days as days with a mean temperature of > 5°C.

Analyses

We calculated the metabolic biomass (MBA) for cervids ($MBA_{cervids}$) and livestock ($MBA_{livestock}$) as the sum of MBA for each herbivore group. Thus, $MBA_{cervids}$ includes $MBA_{semi\text{-}domestic\ reindeer}$, $MBA_{wild\ reindeer}$, MBA_{moose}, $MBA_{red\ deer}$ and $MBA_{roe\ deer}$, while $MBA_{livestock}$ includes MBA_{cow}, MBA_{heifer}, MBA_{horse}, MBA_{sheep} and MBA_{goat}. MBA is given as a grand mean when presenting the results for all different subsets of herbivores (species, species group and the herbivore total) both at the national and the regional level.

We further examined the effect of time (during 1949-1999; six years with 10-year intervals) and biogeographic region (coast, inland and mountain) on MBA for each herbivore species ($N = 10$), herbivore group ($MBA_{cervids}$ and $MBA_{livestock}$) and for all species (MBA_{total}) at the municipality level. Since our main focus was the change in MBA from 1949 to 1999, we used the rate of change ($\Delta MBA = \ln((MBA_{1999}+1)/(MBA_{1949}+1))$) as the response variable.

We give percent browsing (PB) as the proportion of browse relative to MBA_{total}. We examined the rate of change in percent browsing ($\Delta PB = \ln((PB_{1999}+1)/(PB_{1949}+1))$) at both the national and the regional level.

We analysed the variation in ΔMBA and ΔPB by linear models (LM) to examine whether the rate of change differed significantly from 1 (no change). We used ANOVA to examine whether ΔMBA and ΔPB varied among biogeographic regions, and performed all analyses in S-Plus version 6.2. We made maps in ARCGIS using the module ARCMAP.

Results

Total metabolic biomass of livestock and cervids (MBA_{total}) decreased from 126 kg/km^2 unimproved land in 1949 to 107 kg/km^2 in 1999 (85% of the MBA_{total} in 1949; Fig. 2). Changes in MBA_{total} differed between biogeographic regions (Fig. 3). The herbivore pressure in the coastal region was nearly

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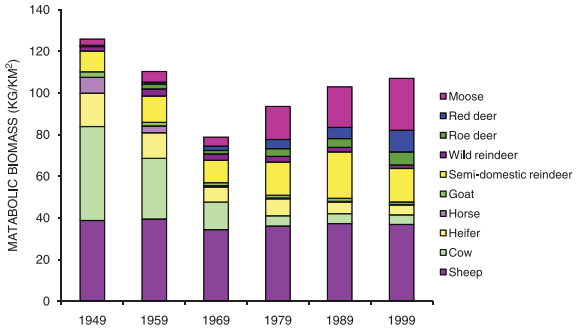


Figure 2. Herbivore pressure in Norway during 1949-1999 measured as metabolic biomass of all large herbivores/(in kg)/km^2 unimproved land (MBA_{total}).

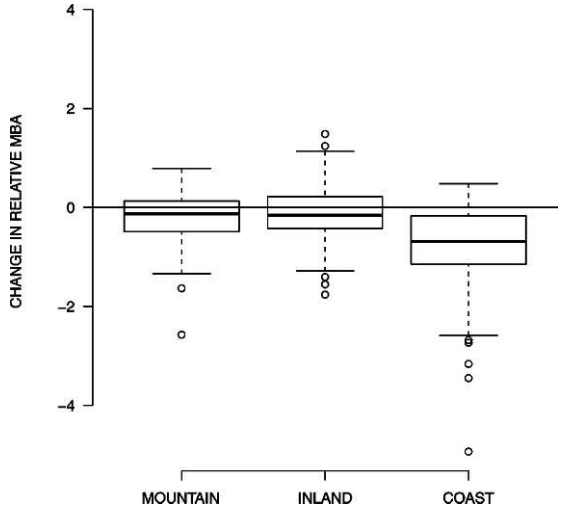


Figure 3. Change in relative herbivore pressure from 1949 to 1999 for all large herbivores in Norway in the mountain, inland and coastal regions. Herbivore pressure is based on metabolic biomass/km^2 unimproved land (MBA_{total}) each year. Note that the y-axis show ln-transformed values.

halved from 1949 to 1999 (54% of the MBA_{total} in 1949), while the decrease was minor in the inland and mountain regions (90 and 92% of the MBA_{total} in 1949, respectively). Although the differences in ΔMBA among regions were significant ($P < 0.001$), most of the change in MBA_{total} from 1949 to 1999 was explained by municipality as compared to region (88 and 12%, respectively; based on the ANOVA sum of squares). Coastal municipalities varied much more in ΔMBA than inland and mountain municipalities ($SE = 0.11$, $SE = 0.04$, $SE = 0.04$, respectively; see Fig. 3). MBA_{total} increased in 135 of 435 municipalities (31%) from 1949 to 1999 (see Fig. 1B).

Livestock grazing ($MBA_{livestock}$) more than halved from 1949 to 1999 (43% of $MBA_{livestock}$ in 1949; from 110.2 to 47.6 kg/km^2). The metabolic biomass of cervids increased by 276% from 1949 (15.8 kg/km^2) to 1999 (59.4 kg/km^2), and cervids were thus the dominant herbivore group in both 1989 and 1999 (55% of MBA_{total}) at the national scale. In 1949, the relative importance of cervids was minor (13% of MBA_{total}). However, while the major decrease in livestock grazing occurred between 1949 and 1969, metabolic biomass of cervids increased mainly from 1979 to 1999. Hence, the total metabolic biomasses showed a bimodal distribution, with lowest grazing pressure in 1969 (63% of MBA_{total} in 1949; see Fig. 2).

All livestock species showed a significant negative rate of change, ΔMBA, from 1949 to 1999 ($P < 0.001$), but ΔMBA differed among biogeographic regions, except for goat ($P = 0.265$; Fig. 4A). Sheep, which were the main livestock grazer in all years from 1969 to 1999, decreased in grazing pressure (MBA_{sheep}) by 5% from 1949 to 1999, mainly due to decreasing MBA_{sheep} in the coastal and inland regions. In contrast, sheep grazing increased by 7% in the mountain region from 1949 to 1999, despite a decrease in the number of grazing days (on unimproved land) in this region. Sheep were still the most important large herbivore in 1999 from a herbivore pressure perspective (MBA_{sheep} constituted 34% of MBA_{total} in 1999). All other livestock were of marginal importance in 1999 (4.3, 4.4, 1.1 and 0.2% of MBA_{total} for cows, heifers, goats and horses, respectively).

All cervids showed a significant positive ΔMBA ($P < 0.001$) from 1949 to 1999, except wild ($P = 0.031$) and semi-domestic reindeer ($P = 0.100$; see Fig. 4B). Correspondingly, $\Delta MBA_{cervids}$ differed between regions except for wild ($P = 0.104$) and semi-domestic reindeer ($P = 0.598$). Semi-domestic reindeer, mainly occurring in the mountain region, had the highest MBA among cervids in all years from 1949 to 1989 ($MBA_{semi\text{-}domestic\ reindeer}$ was 7.8 and 23% of MBA_{total} in 1949 and 1989). MBA_{moose} increased from 2.4% in 1949 to 23.4% of the MBA_{total} in 1999. Thus, moose showed the highest herbivore pressure among cervids in 1999. $MBA_{red\ deer}$ and $MBA_{roe\ deer}$ increased from 0.3 to 9.7% and from 0.1 to 5.9% of MBA_{total}, respectively.

The proportion of browsing vs grazing in Norway increased continuously from 1949 (11%) to 1999

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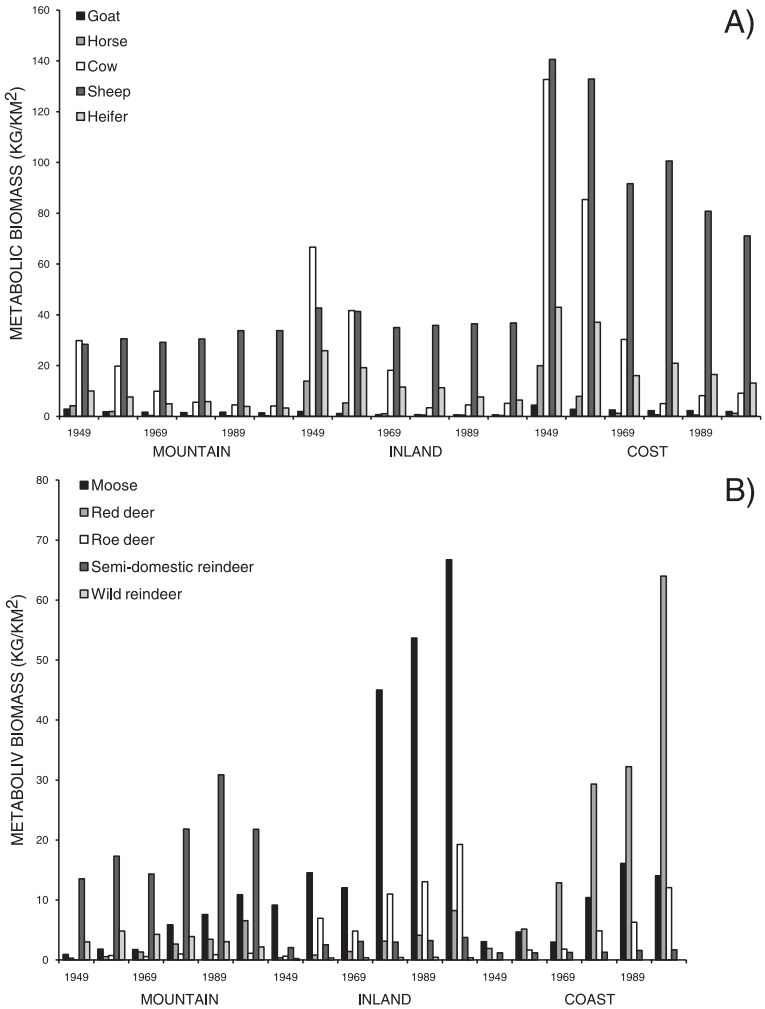


Figure 4. Metabolic biomass (in kg/km^{-2}) for large herbivore species in mountain, inland and coastal regions from 1949 to 1999; A) shows livestock species and B) shows cervids (including semi-domestic and wild herbivores).

(46%). This increase was significant for all biogeographic regions ($P < 0.001$), although the inland municipalities showed a much higher relative increase (l.s. = 0.364, SE = 0.012) compared to coastal (l.s. = 0.183, SE = 0.014) and mountainous municipalities (l.s. = 0.158, SE = 0.006; Fig. 5). Thus, browsing was the dominant foraging pressure in inland municipalities in 1999 (63%), while in 1949 only 11% of the foraging was browsing. In comparison, the relative amount of browsing in 1999 was 30 and 38% in coastal and mountainous municipalities, respectively; increases from 10 and 15% browsing in 1949. The shift in foraging regime was especially evident in southeastern Norway, where the relative consumption of graminoids and herbs decreased from ~ 90 to ~ 10% in several municipalities (Fig. 6).

Discussion

The shift in large herbivore communities in Europe during recent decades, with a strong reduction in free-ranging livestock and a corresponding increase in wild herbivores, has been obvious (Loison et al. 2003, Prins & Gordon 2008). However, quantitative estimates of large herbivore biomass, the relative importance of livestock vs wild herbivores, grazing vs browsing and their spatial and temporal distribution have been missing. This is a paradox given that several herbivore species normally share habitats. The sustainability of herbivory in a given ecosystem thus depends on the total herbivore pressure and the composition of the herbivore community (Albon et al. 2007). Our study provides

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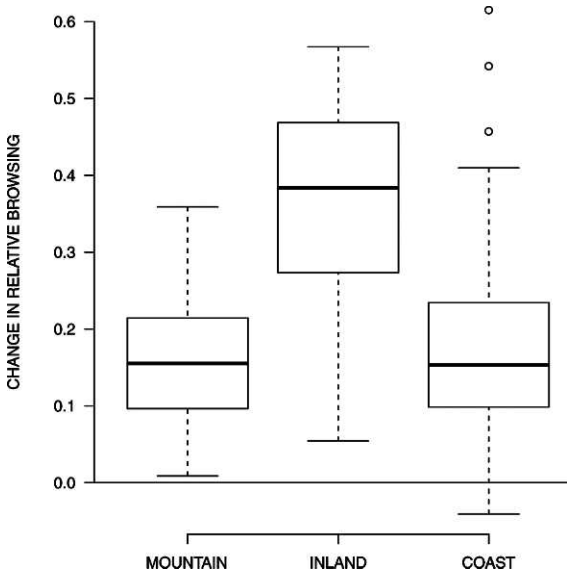


Figure 5. Change in relative browsing (expressed as the proportion of woody fodder vs graminoids and herbs), from 1949 to 1999 in the mountain, inland and coastal regions. Note that the y-axis show ln-transformed values.

an important basis to account for all herbivores in an ecosystem management perspective.

Herbivore pressure and shift from livestock to wild herbivores

The strong decrease of livestock grazing in Norwegian unimproved land from 1949 to 1999 was compensated by an increase in browsing by wild herbivores. The exception is the coastal region, where foraging by large herbivores nearly halved. This may partly be a temporary difference caused by the larger ratio of $MBA_{livestock}$ to $MBA_{cervids}$ at the coast in 1949 than in the mountain and inland regions (see Fig. 4), and thus a longer time needed for cervids to compensate for a given decrease in livestock grazing. Indeed, from 1999 to 2009, the harvest of red deer, mainly inhabiting the coastal region, increased by 70% while the harvest of other cervids was stable or decreasing in Norway (see Fig. S4). However, as both reforestation and encroachment has been substantial, it is unlikely that the coastal region can sustain a similar biomass of wild cervids (mainly red deer) as the livestock dominated biomass in 1949.

While grazing by wild and semi-domestic cervids dominated in the inland region in 1999, the herbivore

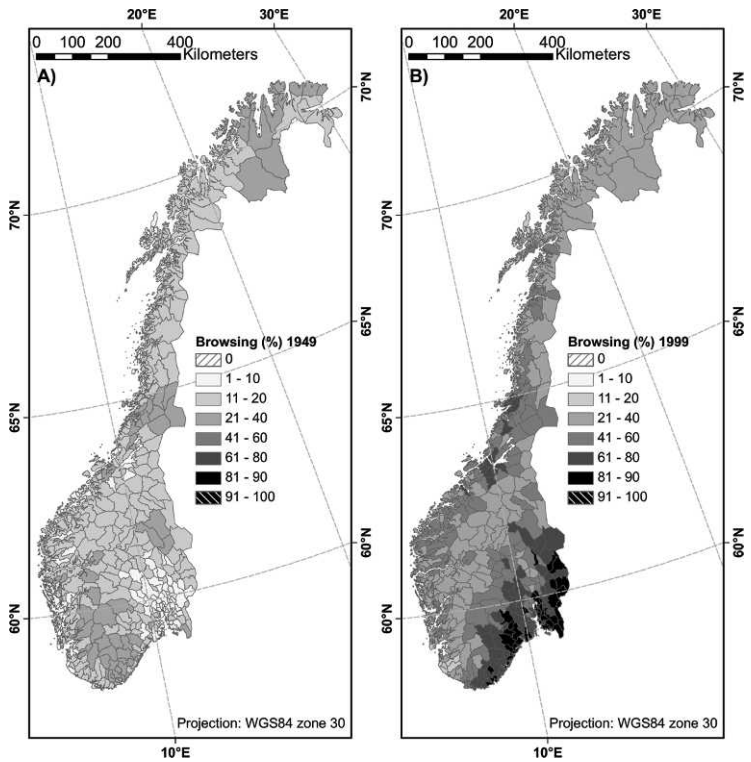


Figure 6. Percent browsing at the municipality level measured as proportion of woody fodder vs graminoids and herbs in 1949 (A) and 1999 (B).

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pressure by livestock and cervids was equal in the mountain and coastal regions. Still, the total number of livestock (i.e. on infields and unimproved land) outnumbered wild and semi-domestic herbivores by 5:1 in 1999 (summer estimates) compared to 17:1 in 1949 (see Table S1). The corresponding ratio measured in MBA was only 7:1 in 1949 and 0.8:1 in 1999.

The large variation in rate of change in total herbivore pressure (ΔMBA), especially among coastal municipalities (see Fig. 3), indicates that ΔMBA may differ between livestock and cervides at the municipality scale. Indeed, the decrease in livestock grazing was not evenly distributed among municipalities, and the corresponding increase in cervid populations did not always occur in the same period or municipality in which the livestock decreased. Total herbivore pressure even increased in 12% of coastal municipalities from 1949 to 1999, mainly because of increasing red deer density. Correspondingly, municipalities with increasing herbivore pressure in the inland region all had a notable increase in moose and roe deer density. Herbivore pressure was more stable in the mountainous municipalities, where reindeer and sheep showed low variation in abundance during the study period.

The bimodal temporal distribution of total herbivore metabolic biomass (see Fig. 2) reveals a time lag in wild herbivore increase after the decrease of livestock. Exploitation competition, mediated through direct or delayed effects of herbivory, is regarded as the most important mechanism for regulating the interaction among herbivore species (Arsenault & Owen-Smith 2002). However, few studies have been able to demonstrate such competitive interactions (Putman 1996, Latham 1999, Richard et al. 2010). Although we have no clear indications that food limitation affected rates of natural mortality or fecundity of cervids in the same period, relaxed competition from livestock as well as reduced use of land for haymaking and collection of fuel wood (Austrheim et al. 2008b) most likely promoted the growth in cervid abundance and might have been a prerequisite of reaching the high levels obtained in more recent years. Evidence of density dependence in individual growth for red deer (Mysterud et al. 2001) and moose (Solberg et al. 2006) suggests that food resources are limiting. However, there is generally a lack of data on how interactions among herbivores ultimately affect the secondary production of sympatric herbivore species (but see Richard et al. 2010), and although a wider range of both plant species and plant parts seems to be eaten with increasing herbivore diversity, the combination of grazers and browsers may lead to a decrease in the total secondary production of herbivores (Prins & Fritz 2008).

More likely than intra-guild competition, we believe that high hunting pressure was the main reason for the low cervid densities at the start of our study period, and the delayed recovery after the decrease in livestock grazing. As in most of Europe (Apollonio et al. 2010), wild cervids in Norway were protected by increasingly restrictive hunting regulations during the 20th century (Andersen et al. 2010). Particularly efficient was the introduction of sex and age-specific quota regulations for moose and red deer in 1968, which relaxed the hunting pressure on adult females. Soon after these regulations, these species, as well as roe deer, increased in density and range distribution (Milner et al. 2006, Austrheim et al. 2008b) until the recruitment rates were again balanced by increasing harvest rates in the 1990s. Only red deer was still increasing in abundance at a national level in 2008 (see Fig. S4). Predation was unlikely to be a significant factor behind the slow increase as large carnivores (i.e. wolves *Canis lupus*, bears *Ursus arctos* and lynx *Lynx lynx*) were almost exterminated by the mid-1900s (Solberg et al. 2003).

Partly for the same reasons, we doubt that the variation in cervid abundance is a result of errors during population reconstruction. Indeed, very unrealistic parameter estimates are to be included in the models to break the temporal pattern reflected in the harvest statistics. This is also the experience from a number of analyses of the dynamics in harvested moose and red deer populations in Scandinavia (see Appendix SIII). However, modelling absolute abundance based on harvest statistics is sensitive to biased parameter estimates, e.g. mortality and recruitment rates (Solberg et al. 2006). Our mortality estimates for moose and red deer are likely to be fairly unbiased at this coarse spatial scale (see Appendix SIII), but less is known about the accuracy of recruitment rates based on hunter observations. Recent studies do, however, indicate that moose hunters observe a rather representative distribution of calves and females (Solberg et al. 2010), and the observed recruitment rates of red deer seem to compare favourably with ovulation rates from harvested red deer females (see

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Appendix SIII). Given the lack of detailed data from all parts of Norway (and also for roe deer), we still believe that the absolute MBA_{cervid} should be interpreted within wide confidence intervals. This has limited consequences as our conclusions are mainly related to the relative spatio-temporal changes in MBA of different species and to a lesser extent their absolute MBA.

Livestock grazing on unimproved land has long traditions all over Europe, and has been a major driver for the maintenance of open semi-natural habitats until the beginning of the 20th century (Wallis de Vries et al. 1998). In Norway, sheep and heifers (34 and 7% of the total herbivore biomass, respectively) are still important large herbivores on unimproved land, and 70% of all sheep fodder consumption occurred on unimproved land during summer in 1999 (Austrheim et al. 2008b). Rough livestock grazing management is maintained especially with sheep and has regionally increased in the UK (Dallimer et al. 2009), the Faroe Islands and Iceland (Austrheim et al. 2008a). Several Mediterranean countries also manage large areas with rough grazing (40 and 38% of the land area in Greece and Spain, respectively; Zervas 1998, Hadjigeorgiou et al. 2005). Despite these exceptions, most of western Europe has experienced the same structural changes in animal husbandry with abandonment and reduced grazing in some areas and a corresponding intensification of animal fodder production in other areas. Rough livestock grazing has especially decreased in more marginal areas with a low proportion of cultivated land (MacDonald et al. 2000, Rook et al. 2004, Hadjigeorgiou et al. 2005). Globally, the area of managed grazing has increased by 600% during the last three centuries, and ca 25% of the global land surface is now used for managed grazing (Asner et al. 2004). However, this increase has mainly occurred in biomes like the savannas, temperate natural grasslands, shrub-lands and deserts, as compared to husbandry systems in western Europe where smaller areas are used more intensively.

Consequences of shifting from grazer to browser dominance

Functional diversity of herbivore communities varies, and spatio-temporal patterns of different grazers, intermediate feeders and browsers are expected to have strong impacts on plant community patterns (Ritchie & Olff 1999). Our study shows that the community of large herbivores in Norway has changed from a (livestock) grazer dominated foraging regime in 1949 to an equal amount of browsing at a national scale in 1999. This shift in foraging regime is especially strong in the lowland region, where foraging on graminoids hardly occurred on unimproved land in southeastern Norway in 1999. Reports on decreasing livestock (Prins & Gordon 2008) and increasing wild herbivore populations (Apollonio et al. 2010) suggest that similar processes are occurring in most of western Europe. Thus, large parts of former rough grazed semi-natural habitats are now developing into habitats for cervids with a higher proportion of browsing. The ecological effects of this functional shift in large herbivore foraging are poorly examined, despite the fact that a high number of red-listed species have their main distribution in semi-natural habitats all over Europe and grazing is considered to be the main land use to maintain such habitats (Wallis de Vries et al. 1998).

The increase of wild cervids in Norway as well as in most of western Europe is exceptional in a historical perspective, and it follows centuries of low cervid densities (Apollonio et al. 2010). Thus, managers have to adapt to wild cervids being the major ecosystem engineers in many landscapes. The shifts from livestock to wild cervids and from grazers to browsers and intermediate feeders are expected to affect the patterns of large herbivore habitat use as well as changes in the vegetation at different spatial scales. For example, graminoids and browse may be distributed differently in the landscape (Gordon 2003) and grazing livestock and wild cervids are often found to forage on different spatial scales (Albon et al. 2007). The foraging behaviour of wild cervids is also more affected by the presence of humans and lack of cover (Mysterud & Østbye 1999). In addition, we suggest that browsing cervids will benefit from the woody encroachment in semi-natural habitats formerly grazed by livestock, which is evident all over Europe (CORINE Land Cover; available at: www.eea.europa.eu/publications/COR0-landcover). Secondary succession in grassland and heathland provides large amounts of woody forage, but only for a limited period. Thus, encroachment may cause time-lagged population dynamics (McCullough 1997, Côté et al. 2004), because eventually, foraging trees grow out of reach and access to fodder decreases.

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Management of large herbivore communities

Most large herbivore species are managed through hunting or animal husbandry (Mysterud 2010). However, because cervids and livestock are typically managed by separate institutions, different operation policies may be an obstacle to a community based herbivore management.

Currently, the European management objectives for wild cervids are changing from a harvest to an ecosystem management perspective (Gordon et al. 2004), and similarly, the arguments for livestock farming (and semi-domestic reindeer herding) are shifting from purely economic to more environmental objectives (Prins & Gordon 2008). This means that the goals for cervid and livestock management are currently merging, but there is still a lack of assessment of the full herbivore pressure from the whole large herbivore community. Indeed, because of fragmented management actions, changes in total herbivore pressure may cause strong negative impacts on preferred forage species (increased herbivory) or increased encroachment (reduced herbivory). In this paper, we show that the total grazing pressure has increased (in 31% of all municipalities) as well as decreased (in 62% of all municipalities) from 1949 to 1999, and in several areas, the sustainability of these changes has been questioned (Mysterud 2006, Solberg et al. 2006, Austrheim et al. 2007, Bråthen et al. 2007, Ims et al. 2007). However, we believe that herbivore management should not only be a question of preventing negative effects of high or low herbivore pressure. The composition of the herbivore community is also important for the facilitation of ecosystem structure and function (Gordon 2006). If semi-natural habitats are to be maintained in their current state, grazing needs to be continued in regions which today are totally dominated by browsing herbivores. Moreover, an increased functional diversity of large herbivores is also found to increase the use of primary production due to a higher range of plant species, individuals and plant parts (Prins & Fritz 2008). This is probably also the reason why a wider range of herbivores with more complementary diets are found to support more plant species as compared to herbivore communities with similar biomass but with a higher diet overlap. However, if management should be able to maintain or even increase herbivore diversity, there is need for dismantling the borders between agricultural and wildlife management and focus more on ecosystem properties such as biodiversity and productivity at the landscape scale.

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