Synergies and trade-offs between ecosystem services in an alpine ecosystem grazed by sheep – an experimental approach

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Abstract

Domestic livestock drives ecosystem changes in many of the world's mountain regions, and can be the dominant influence on soil, habitat and wildlife dynamics. Grazing impacts on ecosystem services (ES) vary according to densities of sheep, but an ES framework accounting for these is lacking. We devised an experiment to evaluate synergies and trade-offs of ESs and components of biodiversity affected by sheep density at the alpine landscape scale in southern Norway. We examined the effects of increased (80 per km^2), decreased (0 per km^2) and maintained sheep densities (25 per km^2) on 'supporting', 'regulating' and 'provisioning' services and biodiversity (plants, invertebrates and birds). Overall, ESs and biodiversity were highest at maintained sheep density. Regulating services, including carbon storage and habitat openness, were particularly favoured by maintained densities of sheep. There was no overall decline in ESs from maintained to increased sheep densities, but several services, such as runoff water quality, plant productivity and carbon storage, declined when grazing increased. Our study provides experimental evidence for a positive effect of grazing on ES, but only at maintained low sheep densities. By identifying ES and biodiversity components that are traded-off at decreased and increased grazing, our study also demonstrates some of the negative impacts on ecosystems that can occur in mountain regions if management does not regulate herbivore densities.

Keywords: herbivory; ecosystem services**;** livestock; management; optimal stocking levels; overgrazing; threshold

Zusammenfassung

Viehhaltung bewirkt in vielen montanen Regionen der Welt Veränderungen am Ökosystem und kann der dominante Einfluss auf die Dynamik von Böden, Habitaten und Wildtieren sein. Die Einflüsse der Beweidung auf Ökosystemdienstleistungen variieren mit der Dichte von Schafen, es fehlt aber ein System der Ökosystemdienstleistungen, das dies berücksichtigt. Wir entwarfen ein Experiment, um die Synergien und Zielkonflikte zwischen Ökosystemdienstleistungen und Biodiversitätskomponenten zu erfassen, die durch die Schafdichte in alpinen Landschaften in Südnorwegen beeinflusst werden. Wir untersuchten die Effekte von erhöhter (80 Ind./km²), verringerter (0 Ind./km²) und beibehaltener Schafdichte (25 Ind./km²) auf "Unterstützungs-", "Regulations-" und "Versorgungsdienstleistungen" sowie auf die Biodiversität (Pflanzen, Wirbellose, Vögel). Insgesamt waren die Ökosystemdienstleistungen und die Biodiversität bei beibehaltener Schafdichte am höchsten. Regulationsleistungen wie Kohlenstoffspeicherung und Offenheit der Habitate wurden durch beibehaltene Schafdichten besonders begünstigt. Es gab keinen generellen Abfall der Ökosystemdienstleistungen von beibehaltenen zu erhöhten Schafdichten, aber verschiedene Dienstleistungen (darunter Qualität des Oberflächenabflusswassers, Pflanzenproduktivität und Kohlenstoffspeicherung) gingen mit zunehmender Beweidung zurück. Unsere Untersuchung belegt experimentell, dass es einen positiven Effekt der Beweidung auf die Ökosystemleistungen gibt, aber nur bei den niedrigen, beibehaltenen Schafdichten. Indem Ökosystemleistungen und Biodiversitätskomponenten identifiziert werden, die bei reduzierter und erhöhter Beweidung unterschiedlich reagieren, zeigt unsere Untersuchung auch einige negative Einflüsse, die in Bergregionen auftreten können, wenn die Herbivorendichten nicht reguliert werden.

Introduction

Livestock grazing affects biodiversity and ecosystem services (ES) across all major biomes, but sustainability is often questioned in areas with high stocking rates. More than 25% of the global land area is managed for grazing (Asner, Elmore, Olander, Martin & Harris 2004), and hence understanding grazing impacts is highly important for sustainable management. Although mountain ecosystems are harsh and often perceived as remote wildernesses, land use and especially livestock grazing has prevailed for thousands of years over most mountain areas, e.g. Scandinavia, UK, Ireland and continental Europe, shaping plant community patterns and generally lowering or completely suppressing the tree-lines (Gehrig-Fasel, Guisan & Zimmermann 2007; Speed, Austrheim, Hester & Mysterud 2010; Tasser, Walde, Tappeiner, Teutsch & Noggler 2007). Land abandonment and reduced livestock densities in mountains in many European countries (MacDonald, Crabtree, Wiesinger, Dax, Stamou et al. 2000) are therefore predicted to be a major driver for ecosystem changes. In contrast, high sheep (*Ovis aries*) densities are still considered to cause overgrazing in some parts of the North-Atlantic region (Ross, Austrheim, Asheim, Bjarnason, Feilberg et al. 2016) and the Central Alps (Meusburger & Alewell 2008).

The strong impact of grazing on ecosystem structure and processes has been well documented, and changes in herbivore densities can lead to both negative and positive effects on biodiversity and the services provided by ecosystems (Côté, Rooney, Tremblay, Dussault, & Waller 2004; Hester, Bergman, Iason, &Moen 2006; Van der Wal 2011). Grazing regimes (i.e. length of the grazing season, species, breeds), habitat characteristics (e.g. productivity, land-use history) and spatio-temporal scale are all important in deciding the actual ecosystem impact of alternative herbivore densities (Milchunas & Lauenroth 1993). However, as most studies contrast heavy grazing with ungrazed exclosures (e.g.

Thompson, MacDonald, Marsden &Galbraith 1995) and experimental gradients of grazing intensity are rarely established, there is a lack of knowledge on how different densities will affect ES and biodiversity and what could be defined as a stocking density for optimising ES.

Independent of herbivore density, grazing may affect all major processes important for the functioning of ecosystems and the services that could be provided, such as primary production, decomposition, nutrient cycling rates and mineralisation (Hobbs 1996). As any grazing regime that sustains some elements of biodiversity and ES could be detrimental for others (Reed 2008), conflicts may emerge from 'optimising' different services. Indeed, the protection of biodiversity for different groups of organisms is often associated with different 'optimal' grazing regimes (Briske, Derner, Milchunas & Tate 2011). Defining sustainable sheep grazing is thus a complex environmental issue which calls for an integrated approach which includes variable grazing regimes and considers a broad range of ecosystem responses. An integrated set-up also allows for a direct comparison on the resulting synergies and trade-offs for biodiversity and ES associated with variable grazing regimes.

In this study, we assess the effects of increased, decreased and maintained (i.e. unchanged) sheep densities on biodiversity and ES in an alpine ecosystem by performing meta-analyses across studies using the same experimental design. This allows for an overall evaluation on how different densities of sheep affect biodiversity and supporting, provisioning and regulating services at the landscape-scale. A key challenge when assessing multiple ES and components of biodiversity within a common framework is ensuring that the most relevant services for ecosystem functioning are included (Millenium Ecosystem Assessment 2005; UKNEA 2011). In our study, 'supporting' services included measures of plant productivity, soil nutrient availability and plant cover which are basic facilities that all other services depend on. ‘Regulating’ services included water quality and storage of soil carbon, together with three indices of vegetation state quantifying habitat openness. The goods that people obtain from ecosystems (‘provisioning’ services) are dependent on supporting and regulating services. In our mountain study system, meat (livestock and wildlife), fodder plants for sheep and reindeer, and fuel-wood are considered the most important provisioning services.

Biodiversity is found to underpin ecosystem functioning and thus the delivery of ES (UKNEA 2011) , although the causal relationships between biodiversity and ES are difficult to assess. Especially supporting and regulating services are found to be positively affected by biodiversity (Balvanera, Pfisterer, Buchmann, He, Nakashizuka et al. 2006). Based on the expectation that moderate grazing will have a positive effect on plant diversity in ecosystems with a long history of grazing (Milchunas, Sala & Lauenroth 1988), we predict higher values of biodiversity and ES at maintained grazing at low densities as compared to decreased grazing. The stocking density “optimum” and herbivore density thresholds where grazing negatively affects biodiversity and ESs are expected to vary among biodiversity components and the services provided by the system, and are thus more difficult to predict (Mysterud 2006). Based on a review of rangeland studies (Briske et al. 2011) we predict higher sensitivity to increased grazing pressure for supporting and regulating services as compared to provisioning services.

Materials and methods

Study area and design

This analysis builds on a unique 11-year experiment on the ecological effects of sheep grazing in an alpine environment of moderate productivity (1602 kg plant biomass per ha in grass dominated habitats, Austrheim et al. 2014). The study site is south-facing and located above the forest-line in Hol, southern Norway (7°55´– 16 8°00´E and 60°40´–60°45´N). Dwarf-shrub heath dominates the vegetation (51%) with lichen ridges (17%), graminoid snow-beds (12%) and tall herb meadow (9%) patchily distributed (Appendix A: Fig. 1).

Nine enclosures (~ 0.3 km^2) running from 1050 to 1320 m a.s.l. were established in 2001 using standard sheep wire fences. Three sheep density treatments, each with three replicates in an experimental block design, were used every summer from 2002: high sheep density (increased), low sheep density (maintained) and no sheep (decreased) representing 80, 25 and 0 sheep per km^2 of grazeable area (Rekdal 2001) respectively (Appendix A: Fig. 1). These densities are within the range of sheep stocking in similar alpine rangelands in Norway. A low density of sheep grazed at the site prior to the start of the experiment in 2001, so the low-sheep density treatment approximately continues the historic grazing pressure. The high sheep density thus represented an increase in grazing pressure, whilst the ungrazed treatment represented a release from grazing pressure. Grazing started in late June and lasted until the first week of September. We used Norwegian white sheep (autumn weights ~ 84 kg and 42 kg for ewes and lambs respectively) – this breed makes up 80% of the ca. 2.1 million sheep grazing in Norway. For more details on the study site and the experimental grazing see (Austrheim, Mysterud, Pedersen, Halvorsen, Hassel et al. 2008).

Assessing grazing effects on ecosystem services and biodiversity

Sheep grazing in mountain environments affects a whole range of different ES that can be classified as provisioning, regulating or supporting ES (Table 1). The only criteria used for selecting studies in the meta-analysis was that they were performed within the experimental set up, and reported an outcome variable that was conceptually linked to the ecosystem service framework. In line with the more recent use of the ES frameworks (e.g. UKNEA, 2011), we have also included biodiversity as an ES with species (birds, beetles, spiders, vascular plants and bryophytes) and family (invertebrates) richness (Table 2). As biodiversity responses to changes in grazing often are indirect and thus slow processes (Olofsson 2006), we included abundance responses to the grazing treatment for birds, voles, beetles, Diptera and Hemiptera (Appendix A: Table 1). Most properties presented in this paper were examined experimentally across the three sheep-grazing treatments and the three blocks. Studies on soil properties (C and N are sampled across treatments within one block) and water quality were only included at increased grazing and decreased grazing in one block.

The approaches used for examining different properties vary both in magnitude and frequency. We have continuous annual data on sheep growth and biennial data on vascular plant community composition and diversity. Soil properties were sampled 5-7 years after the grazing treatment started (2006-2008). Biodiversity data for some of the other species groups (bryophytes, beetles, birds) were sampled at two stages: short (1-2 years) and intermediate (8-10 years) term. Here we use the longer term data when available. The impact of grazing on plant productivity was assessed by the change from 2002 to 2008. Spatial scales of the sampling units (Table 1 & 2, Appendix A: Table 1) also varied from small scales (invertebrates, rodents, most plant and soil properties) to more large scale (birch, birds, sheep), but all properties were sampled across the landscape and thus expected to be representative for the whole experimental site. Exceptions are nitrogen cycling, habitat openness of willow and birch, and lichen cover which are restricted to the mid elevational level, and rodents which were monitored at low elevations only.

The translation from a quantified property to a specific ES is mostly straightforward and in line with the Millennium Ecosystem Assessment framework (MEA 2005). Exceptions are the measure of birch growth (basal area increase) which is used to quantify fuel-wood production classified as a provisioning service. Birch (*Betula pubescens tortuosa*) recruitment (density of birch shoots) is used to quantify habitat openness, classified as a regulating service due to the key importance of landscape openness for several ecological processes (Van der Wal 2011). In this study, the densities of both birch and willow (*Salix* spp.) are considered as dis-services to account for the negative impact of high densities of trees and shrubs on semi-natural species associated with an open landscape. A reduced area with alpine vegetation state defined as the change in range of alpine land is also quantified as a negative regulating service.

Data analysis

Data were extracted from all relevant published studies and two unpublished MSc theses from this experiment. Data from figures were extracted using freely available software (Web Plot Digitizer, Rohatgi (2013). Mean values, standard deviations and effective sample sizes (n = 3 in most cases) were extracted for each of the three sheep grazing treatments for each study. For lamb meat production we calculated total amount of meat produced at each density treatment and calculated standard deviations based on temporal variation (2002-2010). Properties were assigned to ecosystem service types (i.e. supporting, regulating and provisioning services, Table 1) or to biodiversity (Table 2).

Variables assessing the abundance of species or groups were also extracted and these were analysed separately (Appendix A: Table 1).

We performed meta-analyses on each ecosystem service type and biodiversity component for each treatment comparison (maintained density vs. decreased, increased density vs. maintained density, increased density vs. decreased). For each comparison we estimated the bias-corrected standardised mean effect size as the difference between the mean values for each property, standardised by the pooled standard deviation (i.e. Hedges' d standardised mean difference). Since grazing may directly affect variance in a number of properties (Speed, Austrheim, Hester & Mysterud 2013), we did not assume equal variances between treatments (Bonett 2009). All standardised mean differences are presented in the form of the increased density minus the maintained density (i.e. a positive effect size indicates that the ecosystem service is greater at the increased density). We fitted an unweighted fixed effect meta-analytical model using the package metafor (Viechtbauer 2010) within the R statistical environment (R Core Team 2013). We chose an unweighted fixed effects model since our meta-analysis includes data from the same experimental design and on the same alpine ecosystem (in contrast with the more common applications of meta-analyses that synthesise across study populations). Each parameter is represented only once in the models. Typical meta-analyses put greater weight on studies with effect sizes estimated with a higher degree of precision (lower variances). However, in our models the estimates represent different parameters. As the differences in variance between the parameters do not correspond to differential precision in estimating the same parameter, an unweighted approach is more appropriate.

Results

Supporting services

We found no overall differences when comparing grazing treatments across different supporting services (Fig. 1). At decreased vs. maintained density (Fig. 1A), plant cover traded off against plant productivity and N-cycling which were higher at maintained density. At increased vs. maintained densities (Fig. 1B) plant productivity and plant cover traded off against N-mineralisation which peaked at the increased density treatment. A similar pattern appeared when comparing decreased with the increased density treatment (Fig. 1C): plant cover and plant productivity traded off against both N-mineralisation and N-cycling which were higher at increased sheep densities.

Regulating services

Regulating services showed higher values at maintained densities of sheep as compared to the decreased treatment ($p = 0.008$, Fig. 1A). Habitat openness from birch and willow as well as the range of alpine land at maintained densities were the main contributing services providing more regulating services at maintained density vs. decreased treatment. Increased as compared to maintained density also scored high on range of alpine state and habitat openness from birch, but tended to be traded off against carbon storage in soils of both grassland and snowbeds. No overall differences in regulating ES between treatments could be found between increased and maintained densities (Fig. 1B). Regulating services were marginally higher at increased densities ($p = 0.069$, Fig. 1C) than at decreased densities, pointing to the positive values of habitat openness and range of alpine land, but traded off against water quality and C storage in snowbed soils which was higher at the decreased treatment.

Provisioning services

Provisioning services showed marginally higher values at maintained ($p = 0.063$) as compared to the decreased treatment (Fig. 1A). The main provisioning service at maintained densities was livestock meat production which traded off against fuel-wood production at the decreased treatment. Marginally higher values at increased than maintained densities of sheep ($p = 0.088$, Fig. 1B) were also driven by livestock meat production, graminoid abundance (reindeer summer fodder) and birds for hunting, while reindeer winter fodder and fuel-wood production were higher at maintained sheep densities. Similar trade-offs appeared when comparing provisioning services at decreased and increased density treatments, but with clearer contrasts between livestock meat production (at increased densities) and availability of reindeer winter fodder and fuel-wood (at decreased densities).

Assessing effects of grazing treatments across all types of ES

Maintained sheep densities had a higher overall value for provision of the measured ES as compared to the decreased treatment ($p = 0.002$; Fig. 1 A). No differences were found between increased and maintained densities of sheep ($p = 0.312$) while increased densities were marginally higher than the decreased treatment ($p = 0.097$).

Biodiversity

An overall assessment showed no differences in species richness between grazing treatments across different taxa (Fig. 2A, B, C). In general, grazing had minor effects on species richness for birds, invertebrates and plants. Exceptions were spider richness, which decreased at increased sheep densities compared to both maintained densities and the decreased treatment (Fig. 2 B, C), and bryophyte species richness which was higher at maintained densities compared to increased (Fig. 2 A).

Assessing effects of grazing treatments across all types of ES and biodiversity

Maintained sheep densities had a higher overall value for provision of the measured ES and biodiversity as compared to the decreased treatment ($p = 0.002$). Increased densities had marginally higher biodiversity and ES than the decreased ($p = 0.090$). No differences were found between increased and maintained densities of sheep ($p = 0.378$).

Grazing effects on abundances of animal species

Overall, maintained sheep density had a positive effect on abundances (i.e. number of individuals, density or population growth rate) of animal species ($p = 0.023$), as compared to the decreased treatment (Appendix A: Fig. 2A). Total bird density, density of insect eating birds, field vole population growth and abundances of a beetle species (*Byrrhus fasciatus*) and Hemiptera all responded positively at maintained densities as compared to the decreased treatment, while none of the other animal taxa traded-off at plots with decreased densities.

Discussion

Mountain rangelands have many functions and provide many ecosystem services underpinned by biodiversity (Millenium Ecosystem Assessment 2005; UKNEA 2011). However, a common definition of a sustainable grazing regime (i.e. number of sheep recommended to graze at upper and lower density limits, at a given productivity) needs to be underpinned by experimental evidence showing how different ecosystem functions and services are affected by grazing. Our meta-analysis of experimentally-varied grazing in a mountain ecosystem included a wide range of biodiversity components and services that are important for ecosystem support, regulation and provisioning. The overall assessment showed a net positive effect of grazing at maintained low densities compared to the treatment where sheep were removed. This positive effect was even clearer if data on species abundances, densities and population growth rate were included in the overall analysis. In particular, regulating services were favoured by grazing at maintained low densities. We found no overall decrease in biodiversity and ES when sheep densities were increased, but a broad range of services belonging to all main service types showed a decrease.

Synergies and trade-offs within and between ES and biodiversity components

Within provisioning services measured, the clearest trade-off was found between livestock meat and fuel-wood (birch) production when comparing both increased and maintained sheep densities vs. decreased grazing. This trade-off is expected because both willow and birch are frequently eaten by sheep (Mobæk, Mysterud, Holand & Austrheim 2012a), and reflects an important change to the alpine ecosystem following grazing cessation, which is especially clear and rapid below the climatic tree-line (Hofgaard 1997; Speed et al. 2010).

The key importance of grazing impact on trees and shrubs is also reflected in the increase in habitat openness and proportion of alpine land. These regulating services were, however, traded-off against water quality and partly carbon storage at increased sheep density vs. decreased grazing. Although it is well known that high densities of livestock can negatively affect carbon storage and water quality (Briske et al. 2011; Van der Wal 2011), the study by Martinsen, Mulder, Austrheim and Mysterud (2011b) included in this meta-analysis showed that carbon storage tended to increase at maintained low vs. increased densities which reveals a possible density threshold for grazing impacts on carbon. Trade-offs within supporting services were driven by a grazing-induced decrease in plant cover while plant productivity, N-cycling and mineralisation increased with grazing, although thresholds differed among properties.

Trade-offs between the main types of services are less clear from this study. No trade-offs were found between provisioning services such as livestock at maintained low or increased densities and the more basic supporting and regulating services, which is often the case in human-manipulated rangelands (Rey Benayas & Bullock 2012; UKNEA 2011; Van der Wal 2011). On the contrary, this study points to the synergies between regulating and provisioning services at maintained low sheep densities. In addition, most supporting services showed synergies with regulating and provisioning services at maintained vs. decreased grazing, the only exception being plant cover. At increased densities, supporting services tended to decrease with a reduction in both plant cover and plant productivity as compared to both maintained densities and decreased grazing.

Overall, no services showed a decrease over time at maintained low sheep densities during this experiment (G. Austrheim, unpublished results), while services such as carbon storage, plant productivity and nutrient cycling tended to be facilitated by low densities in the grassland habitats as compared to both decreased and increased densities. The positive effects of low sheep densities found in this study support the intermediate disturbance hypothesis (Connell 1978; Grime 1973), and the hump-shaped grazing response predicted for plant diversity in productive ecosystems with a long history of grazing (Milchunas et al. 1988). Further support comes from a large number of plant studies [see reviews by Olff and Ritchie (1998), Cingolani (2005)] and studies on birds, mammals and some groups of invertebrates [see review by Van Wieren and Bakker (2008)].

Potential mechanisms for positive effects of grazing on biodiversity and ES have been linked to herbivore-mediated increased N-cycling and mineralisation (Harrison & Bardgett 2008), which can increase resource availability in alpine systems with high N limitation (Budge, Leifeld, Hiltbrunner & Fuhrer 2011). Indeed, grazing caused an increase in both these supporting services in our study while plant productivity marginally increased at maintained low densities. Moreover, positive interactions among biodiversity components are expected to be found, especially in harsh environments as predicted by the "stress gradient hypothesis" (Bertness & Callaway 1994). Such synergies are shown among plants, which may ameliorate abiotic conditions (Callaway, Brooker, Choler, Kikvidze, Lortie et al. 2002), but also herbivores may facilitate each other when grazing increases quality or quantity of forage (Barrio, Hik, Bueno & Cahill 2013) e.g. in our study system, field vole abundance and lamb weight tended to respond positively at maintained low densities of sheep compared to increased densities (Mobæk, Mysterud, Holand & Austrheim 2012b; Steen, Mysterud & Austrheim 2005).

Spatio-temporal effects of grazing

As grazing involves both direct (grazing, trampling) and indirect (change in competitive interactions) ecosystem effects, differences in time scale and magnitude of grazing responses among ecosystem properties are expected (Olofsson 2006). More abrupt responses to changes in grazing regime, such as birch recruitment at decreased grazing (Speed et al. 2010), are often found to stabilise over time (Olff, Vera, Bokdam, Bakker, Gleichman et al. 1999). This meta-analysis used long term data when available, but for some invertebrates and birds, grazing affected species richness differently on short vs. longer-term scales (Austrheim et al. unpublished results). Nevertheless, alpine ecosystems are known to vary independently of grazing (Körner 2003), and this is clearly shown by the inter-annual variation in sheep weight (Mobæk et al. 2012b), birch growth (Speed, Austrheim, Hester & Mysterud 2011b) and plant demography (Evju, Halvorsen, Rydgren, Austrheim & Mysterud 2010, 2011). For this reason, single time-period measures and measures repeated only two times with contrasting effects must be used with caution.

Spatial variation at almost any scale is expected to affect ecosystem responses to grazing (Olff et al. 1998). A central question is whether grazing overrides other environmental variation (Stohlgren, Schell & Vanden Heuvel 1999) and homogenises the landscape. The data included in this meta-analysis showed no effect of grazing on vascular plant diversity. However, other studies at the site have shown that the impact of grazing on diversity varies along the elevational gradient (Speed et al. 2013b). Therefore a more thorough understanding of the impact of grazing on ES and biodiversity would need to account for elevational variation in responses.

Climate change is expected to mediate spatio-temporal effects of grazing in several ways involving both biotic and abiotic changes. For example, increased temperatures (i.e. > mean long term summer temperature, Speed et al. 2011b), evident for all study years at the site, could drive an upward shift of lowland plants along the elevational gradient (Speed, Austrheim, Hester & Mysterud 2012), but could also reduce snow cover important for the availability of high quality forage in late summer for herbivore body growth (Mysterud & Austrheim 2014).

Management implications

In Europe, the arguments in favour of livestock grazing are shifting from being purely economic to being more broadly geared towards the environment (Gordon & Prins 2008). The overview of synergies and trade-offs within a common framework presented here should serve to facilitate grazing management decisions across a broader range of ES and biodiversity. If implemented well, grazing can sustain many ecosystem functions and services in the longer term, including high meat production per lamb which is important for the livestock economy. The mixed impacts of sheep grazing on different ES, however, challenge management priorities and trade-offs. For example, if it is desirable to prevent transitions to forests in mountains, and maintain biodiversity and ecosystem services associated with the open landscape, there needs to be continued grazing as a management strategy. Even short term cessation of grazing will allow birch to grow out of sheep browsing reach in productive environments (Speed, Austrheim, Hester & Mysterud 2011a), but low densities of sheep in these alpine systems were both sufficient to maintain open land (Speed et al. 2010) and to benefit delivery of several ES. Such herbivore density thresholds at which decreased or increased grazing negatively affect biodiversity and processes important for ecosystem functioning have in part been assessed by a few studies (Côté et al. 2004; Mysterud 2006; Van Wieren et al. 2008; Wallis de Vries, Bakker & van Wieren 1998), though there is little on ES. Our study indicates that this herbivore density threshold will vary among services. Several biodiversity components and ES for all main types of services including provisioning declined in these productive alpine ecosystems when densities increased from the maintained low treatment, even if there is no overall decrease in ES and biodiversity. A flexible (learning) management regime with repeated surveys on key properties such as selected forage species (Evju, Mysterud, Austrheim & Økland 2006) could be a useful approach for grading of herbivore densities to 'optimise' the production of desired ecosystem services in mountain ecosystems.

Prioritisation choices when trade-offs are identified can be highly challenging, as management evaluations are often value-laden (Millenium Ecosystem Assessment 2005). First, should managers favour semi-natural and alpine species associated with open grazed landscapes, or birch forest species associated with grazing cessation? Although we have classified birch encroachment as a negative process for this paper, this could also be evaluated as positive depending on whether fuel-wood and a sub-alpine birch forest or an open semi-natural habitat with grazing resources is preferred. Afforestation may also lead to increased use by moose (*Alces alces*) and red deer (*Cervus elaphus*) in these areas, which is important for e.g. game meat production. Recent assessments of environmental conditions and impacts for red-listed species provide arguments for preventing birch recruitment in alpine land (Austrheim, Bråthen, Ims, Mysterud & Ødegård 2010). Vertebrate herbivores could buffer climate-driven expansions of trees and shrubs (Post, Forchhammer, Bret-Harte, Callaghan, Christensen et al. 2009) and thus promote persistence of red-listed species, especially small-statured plants associated with semi-natural and alpine landscapes. Second, should managers favour high total meat production or high production per lamb (which decreases from high to low sheep densities) (Mobæk et al. 2012b)? This is a well-known trade-off for grazing management (Briske et al. 2011) and overgrazing is a main challenge for sustainable management of livestock globally (Asner et al. 2004). Our study also illustrates some of the negative ecosystem effects which can appear at certain grazing density thresholds, and identifies services that are traded-off if density thresholds are reached or exceeded.

Our study shows how management of livestock grazing could move towards a greater focus on broader environmental issues as well as production, by considering explicitly how biodiversity and ecosystem services could be balanced against the more traditionally valued provisioning services of livestock meat production. This would be a powerful way forward for grazing management globally.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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Table 1. An overview of specific services included in the study associated with either supporting, regulating or provisioning service types.

Service type	**Specific service**	**Study species or group**	**Units**	**Study period**	**Elevational level**	**Vegetation type**	**Effective sample size_D***	**Effective sample size_M§**	**Effective sample size_I§§**	**Reference**	**Data extracted from**
Supporting	Plant productivity	Vascular plants	Change in g per m^2	2002-2008	1050-1320 m a.s.l.	Grassland (graminoid snow bed, tall herb meadow)	3	3	3	Austrheim et al. (2014)	Fig. 2
Supporting	Plant cover	Plant	Percent	2005	1050-1320 m a.s.l.	No specific vegetation type	3	3	3	Austrheim et al. (2008)	Fig. 3
Supporting	Nitrogen mineralisation	Inorganic soil N	µg g soil	2007-2008	1050-1320 m a.s.l.	Grassland (graminoid snow bed, tall herb meadow)	25	25	32	Martinsen et al. (2012)	Fig. 3
Supporting	Nitrogen cycling	*Avenella flexuosa*	% per g plant N-pool and m^2.	2009	Mid elevation, 1168 m a.s.l.	Tall herb meadow	26	26	26	Martinsen et al. (2011a)	Fig. 3
Regulating	Water quality	*E. coli*	Most probable number per 100 ml	2006-2008	Mid elevation, 1200 m a.s.l.	No specific vegetation type	17	NA	20	Martinsen et al. (2013)	Table 2
Regulating	Habitat openness from willows	*Salix* spp.	No shoots per 10 m transect	2010	Mid elevation, 1200 m a.s.l.	No specific vegetation type	3	3	3	Speed et al. (2013)	Fig. 3
Regulating	Habitat openness from birch	Birch	Proportion of transect segments occupied by birch	2009	Mid elevation, 1200 m a.s.l.	No specific vegetation type	3	3	3	Speed et al. (2010)	Fig. 2
Regulating	Carbon storage - snowbed soils	Soil organic carbon	% of fine earth	2008	1050-1320 m a.s.l.	Graminoid snowbed	17	17	18	Martinsen et al. (2011b)	Table 1 and Fig. 2a
Regulating	Carbon storage - grassland soils	Soil organic carbon	% of fine earth	2008	1050-1320 m a.s.l.	Tall herb meadow	8	8	14	Martinsen et al. (2011b)	Table 1 and Fig. 2a

Regulating	Alpine vegetation state	Plant community composition	Elevational shift in m over time	2001-2009	1050-1320 m a.s.l.	Grassland (graminoid snow bed, tall herb meadow)	3	3	3	Speed et al. (2012)	Fig. 4 a
Provisioning	Reindeer winter fodder	Lichen	Percent	2005	Mid elevation, 1200 m a.s.l.	Lichen heath	5	5	5	Mysterud & Austrheim (2008)	Fig. 2a
Provisioning	Livestock meat production	Sheep (lamb)	Mean weight (kg) over time per treatment	2002 to 2010	1050-1320 m a.s.l.	No specific vegetation type	3	3	3	Mobæk et al. (2012b)	Result
Provisioning	Large herb abundance	*Solidago virgaurea*	Change of frequency	2001-2005	1050-1320 m a.s.l.	No specific vegetation type	3	3	3	Mysterud & Austrheim (2008)	Fig. 1b
Provisioning	Graminoid abundance	*Carex bigelowii*	Change of frequency	2001-2005	1050-1320 m a.s.l.	No specific vegetation type	3	3	3	Mysterud & Austrheim (2008)	Fig. 1a
Provisioning	Birds for hunting	Willow grouse	n per km^2	2005	1050-1320 m a.s.l.	No specific vegetation type	3	3	3	Loe et al. (2007)	Fig. 1
Provisioning	Fuel-wood production	Birch	Tree basal area growth	2010	1050-1320 m a.s.l.	No specific vegetation type	3	3	3	Speed et al. (2011b)	Fig. 3a

*D = Decreased

§M= Maintained

§§I= Increased

Table 2. An overview of biodiversity components included in the study. All parameters are given as richness for species or insect families at a given year. Effective sample size = 3 for all treatments.

Study species or group	**Specific service**	**Units**	**Study year**	**Reference**	**Data extracted from**
Spiders	Species richness	N	2003	Mysterud et al. (2010)	Fig. 1b
Vascular plant	Species richness	N	2005	Austrheim et al. (2008)	Table A5
Bryophytes	Species richness	N	2005	Austrheim et al. (2008)	Table A5
Birds	Species richness	N	2005	Loe et al. (2007)	Fig. 2
Beetles	Species richness long term	N	2009	Rønning (2011)	Fig.11
Invertebrate	Insect family richness	Mean number	2002	Mysterud (2005)	Table 1

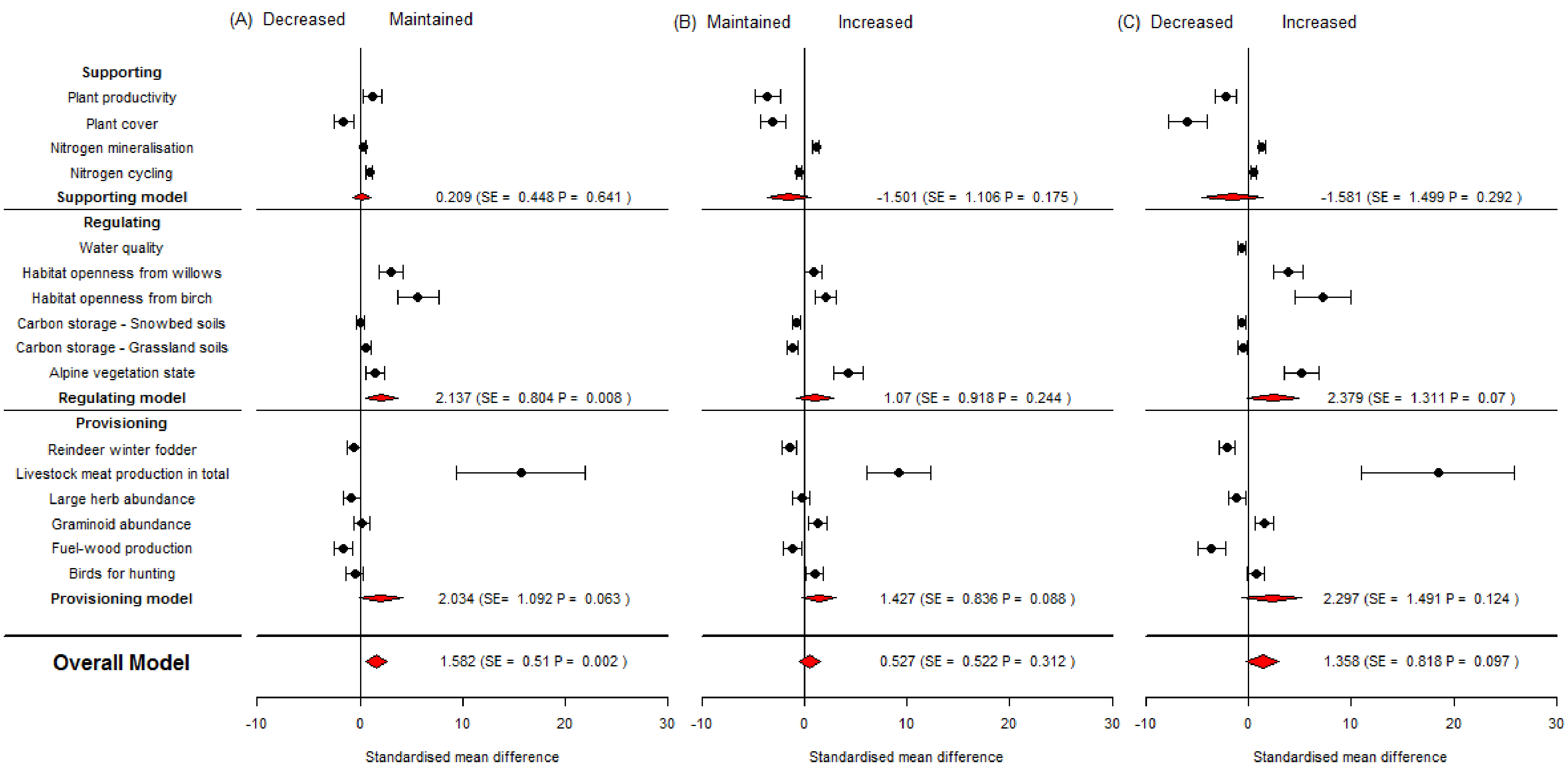
Figures

Fig. 1. (A) decreased vs. maintained, (B) maintained vs. increased, and (C) decreased vs. increased. Grazing effects on ecosystem services calculated as effect size (standardised mean difference and standard errors) for each pair of treatments: decreased vs. maintained, maintained vs. increased, decreased vs. increased. A positive effect size for column (A) indicates that the ES is higher at the maintained density of sheep than the decreased density of sheep. Results of the overall model are shown in the last row.

Fig. 2. (A) decreased vs. maintained, (B) maintained vs. increased, and (C) decreased vs. increased. Grazing effects on biodiversity calculated as effect size (standardised mean difference and standard errors) for each pair of treatments: decreased vs. maintained, maintained vs. increased, decreased vs. increased. A positive effect size for column (A) indicates that the biodiversity component is higher at the maintained density of sheep than the decreased density of sheep. Results of the overall model are shown in the last row.

Appendix A: Fig. 1. Overview of the experimental site at Hol in southern Norway showing grazing treatments and vegetation types. 100 m contour lines are shown. UTM coordinates are in zone 32V.

Appendix A: Fig. 2. Grazing effects on animal species abundances, densities and population growth rates calculated as effect size (standardised mean difference and standard errors) for each pair of treatments: decreased vs. maintained, maintained vs. increased, decreased vs. increased. A positive effect size for column (a) indicates that the abundance measure is higher at the maintained density of sheep than the decreased density of sheep. Results of the overall model are shown in the last row.



(A) Decreased Maintained
(B) Maintained Increased
(C) Decreased Increased
Supporting
Plant productivity
Plant cover
Nitrogen mineralisation
Nitrogen cycling
Supporting model
0.209 (SE = 0.448 P = 0.641)
-1.501 (SE = 1.106 P = 0.175)
-1.581 (SE = 1.499 P = 0.292)
Regulating
Water quality
Habitat openness from willows
Habitat openness from birch
Carbon storage - Snowbed soils
Carbon storage - Grassland soils
Alpine vegetation state
Regulating model
2.137 (SE = 0.804 P = 0.008)
1.07 (SE = 0.918 P = 0.244)
2.379 (SE = 1.311 P = 0.07)
Provisioning
Reindeer winter fodder
Livestock meat production in total
Large herb abundance
Graminoid abundance
Fuel-wood production
Birds for hunting
Provisioning model
2.034 (SE= 1.092 P = 0.063)
1.427 (SE = 0.836 P = 0.088)
2.297 (SE = 1.491 P = 0.124)
Overall Model
1.582 (SE = 0.51 P = 0.002)
0.527 (SE = 0.522 P = 0.312)
1.358 (SE = 0.818 P = 0.097)
-10 0 10 20 30
Standardised mean difference

Fig. 1

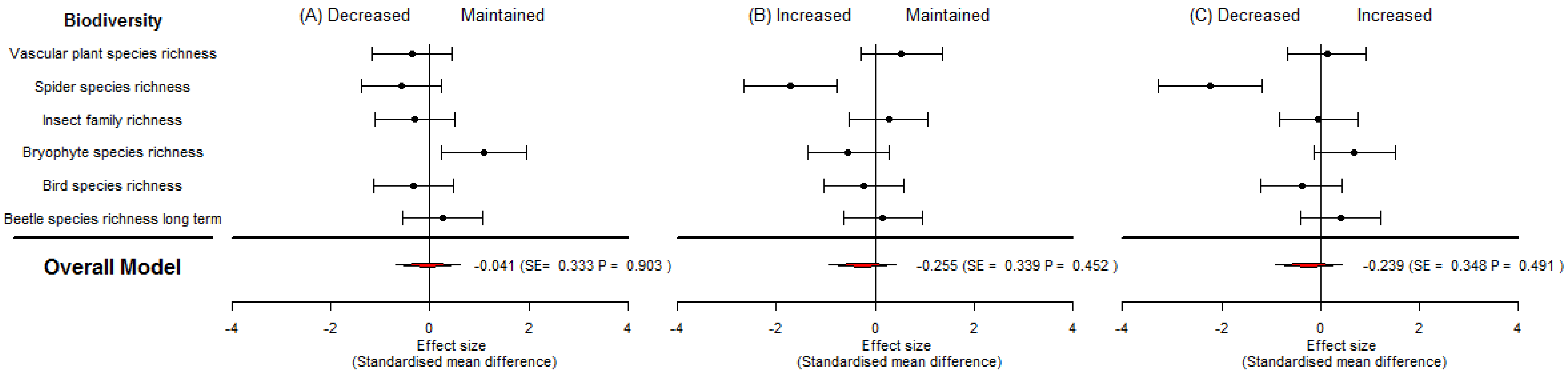

Biodiversity
(A) Decreased
Maintained
(B) Increased
Maintained
(C) Decreased
Increased
Vascular plant species richness
Spider species richness
Insect family richness
Bryophyte species richness
Bird species richness
Beetle species richness long term
Overall Model
-0.041 (SE= 0.333 P = 0.903)
-0.255 (SE = 0.339 P = 0.452)
-0.239 (SE = 0.348 P = 0.491)
-4
-2
0
2
4
Effect size
(Standardised mean difference)

Fig. 2