SR13
A Systematic Review

MISTRA EviEM
EVIDENCE-BASED ENVIRONMENTAL MANAGEMENT

EviEM Summary 2018

Claes Bernes
Biljana Macura
Bengt Gunnar Jonsson
Kaisa Junninen
Jörg Müller
Jennie Sandström
Asko Lõhmus
Ellen Macdonald

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Cover: Moose (*Alces alces*) are among the most important herbivores in Swedish forests.
Photo: Anna Fuster / Creative Commons.

Manipulating ungulate herbivory: Effects on forest biodiversity

Summary of Systematic Review SR13

By Claes Bernes, Biljana Macura, Bengt Gunnar Jonsson, Kaisa Junninen, Jörg Müller, Jennie Sandström, Asko Lõhmus and Ellen Macdonald

Executive summary

The primary aim of the systematic review that is summarised here was to examine how forest vegetation and invertebrates are affected by manipulation of the grazing/browsing pressure by livestock or wild ungulates. The ultimate purpose was to investigate whether such manipulation is useful for conserving or restoring biodiversity in forest set-asides.

We considered studies of manipulated ungulate herbivory in forests anywhere within the boreal and temperate zones, not only in protected areas but also in production forest. Most of the 144 studies included in the review had been conducted in North America, Europe or Australia/New Zealand. The intervention most commonly studied was experimental exclusion of wild and/or domestic ungulates by fencing.

We found negative effects of herbivory on the abundance of understorey vegetation as a whole, woody understorey and bryophytes, and also on the species richness of woody understorey vegetation, whereas the richness of forbs and bryophytes was favoured. Several effects depended on whether the ungulates were native, introduced or domesticated, but the duration and intensity of herbivory manipulation had limited influence.

Among invertebrates we found negative effects of herbivory on the abundance of lepidopterans and spiders, but no significant effects on species richness.

Our review confirmed that manipulation of ungulate herbivory is often highly influential on tree regeneration and on the abundance, diversity and composition of understorey vegetation.

We also identified important knowledge gaps – we found few studies of boreal areas, long-term herbivory effects, impacts on bryophytes, lichens and invertebrates, and effects of manipulation less radical than total exclusion of ungulates.

Fig. 1. Some of the studies included in the review examined biodiversity effects of sustained livestock grazing in forests. Comparisons were made between areas long grazed by domestic animals and areas that were long ungrazed or where grazing had been abandoned. - Photo: Creative Commons.

Manipulation of herbivory as a tool for biodiversity conservation

Most forest regions host large mammalian herbivores as part of their native fauna, and these animals have important effects on forest structure, composition and biodiversity.

In many areas, human activities have greatly influenced the abundance and species composition of large herbivores. Such activities include the introduction of livestock grazing, introductions and regulation of game species, removal of top predators, and provision of supplementary forage. In some cases, interventions of these kinds have resulted in either very high or very low herbivory pressure.

'Overabundance' of native wild herbivores has frequently been identified as a major challenge for forest regeneration and biodiversity conservation, and livestock grazing too is often perceived as being in conflict with the aims of both forestry and forest conservation.

On the other hand, a lack of mammalian herbivores can also pose challenges for conservation management. Indeed, livestock grazing has been used to help compensate for the loss of open natural habitats in the profoundly transformed European landscapes. Further, managed livestock grazing has been used to restore ecosystems that have become degraded due to a lack of wildfire, and has also been considered beneficial by improving nutrient cycling, controlling ground vegetation that competes with trees, and reducing fire risks.

Management of mammalian herbivory can, therefore, be a critical tool for biodiversity conservation. This can be especially true in forest set-asides, in which the current abundance and species composition of herbivores are often influenced by past management or by the isolated nature of protected areas.

However, there has been a shortage of quantitative assessments of the effects of grazing and browsing on forest biodiversity. Consequently, there was not sufficient evidence to make informed decisions on regulation of wild herbivores or livestock to meet specific conservation targets in protected forests.

We have therefore conducted a *systematic review* within this field, focusing it on impacts of wild and domestic ungulates on vegetation and invertebrates in temperate and boreal forests. Ungulates include all species of deer and other cervids, and also livestock such as cattle, sheep, goats, horses and their relatives in the wild.

The broad aim of our review was to understand whether actively managing mammalian herbivore pressure in forest set-asides can help achieve conservation objectives. We drew on studies of exclusion, enclosure or culling of wild ungulates, and also on studies of forest grazing by livestock.

What is a systematic review?

In this review, we used a systematic methodology to synthesise available evidence on effects of forest grazing/browsing. Systematic reviews are summaries of existing research – in this respect, they do not differ from ordinary literature reviews. The difference lies, instead, in their rigour, transparency and comprehensiveness. A systematic review is characterised by meticulous planning, thorough searches for literature, objective assessments of studies, and a complete documentation of the whole review process. This approach is designed to increase reliability and repeatability and to avoid bias. Many systematic reviews include quantitative conclusions based on meta-analysis, a statistical technique for aggregating results from multiple studies.

In addition to examining the impacts of manipulated vs. unmanipulated herbivory on forest structure, tree regeneration, understorey vegetation and invertebrates, our review addressed the following specific questions:

- How do the impacts of herbivory manipulation vary with its duration and with the abundance, origin (native/introduced/domestic) and feeding strategy (e.g., grazer or browser) of the main herbivores?

- How do impacts of herbivory manipulation vary with the geographical context and habitat?

Synthesis of a large body of evidence

The review included a total of 144 studies. Slightly more than half of these were conducted in North America, whereas the other studies were mostly carried out in Europe. Temperate broadleaf/mixed forest was the most frequently represented forest cover type, being examined by 80 studies. Hence, while parts of the temperate and boreal zones were well-covered by studies, others were not. In particular, we found no studies from boreal regions in Asia and few from the North American boreal forest.

Fig. 2. In most of the studies included in the review, herbivory had been manipulated by means of fencing. The fences usually excluded all ungulates, and comparisons were made of biodiversity inside and outside the exclosures. Photo: Nicholas A. Tonelli / Creative Commons.

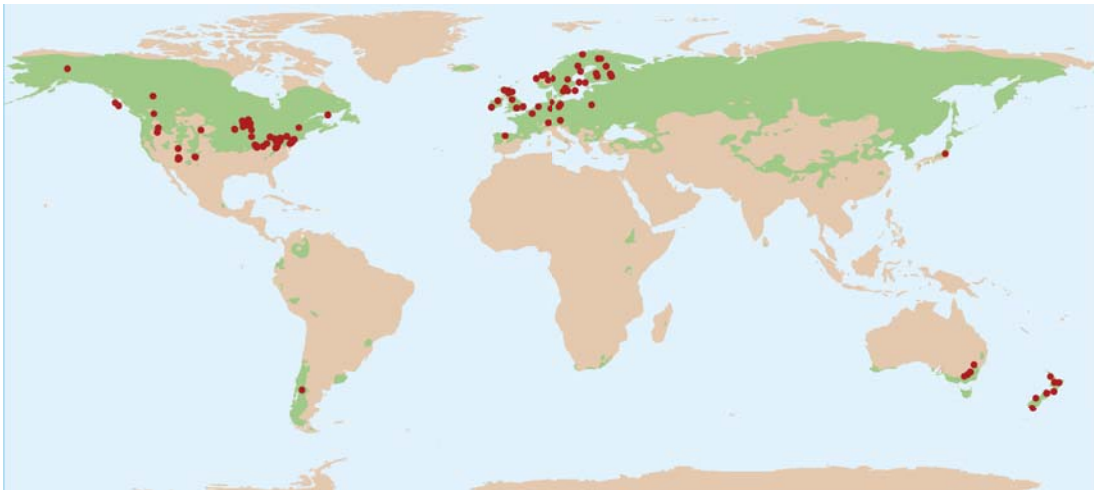

Fig. 3. The red dots on the map show the locations of studies included in the review. The green colour indicates the extent of the boreal and temperate climate zones. The table below shows the number of included studies per country.

USA	64	Germany	6	Japan	1
Sweden	14	Norway	6	Netherlands	1
Canada	11	Australia	4	Poland	1
Finland	11	Ireland	3	Russia	1
New Zealand	10	Argentina	1	Spain	1
UK	9	France	1	Switzerland	1

The intervention most commonly studied (118 cases) was complete exclusion of wild and/or domestic ungulates by means of fencing, usually (but not always) carried out for experimental purposes. Sizes of ungulate exclosures ranged from 0.5 m^2 to 2,428 ha, with a median of 400 m^2. Comparisons were made of the flora and/or fauna inside and outside exclosures. In eight studies, fenced enclosures were used to keep ungulates at controlled densities lower and/or higher than the ambient mean.

Other studies were mainly observational: 17 of them examined effects of 'sustained/abandoned/resumed livestock grazing' (meaning that they compared forested areas long grazed by domestic animals to areas that were long ungrazed or where grazing was abandoned, or that they examined areas before and after resumption of livestock grazing), whereas six studies investigated effects of culling of wild ungulates.

The duration of herbivory manipulation (the time elapsed from start of manipulation to final measurement of effects) ranged from 1 to 92 years in studies based on fencing (exclusion or enclosure) of ungulates, with a median of 6 years. In studies of sustained/abandoned/resumed livestock grazing, it was often uncertain or unknown how long the current grazing system had persisted. Reported estimates varied from 7–8 to 20–70 years, with a median around 20 years.

In 62 studies the manipulated ungulate populations were dominated by white-tailed deer (*Odocoileus virginianus*) or mule deer (*O. hemionus*). Red deer (*Cervus elaphus*), elk (*C. canadensis*) or sika deer (*C. nippon*) were the dominant (or co-dominant) ungulates in 34 studies, roe deer (*Capreolus capreolus*) in 17 studies, moose (*Alces alces*) in 10 studies, fallow deer (*Dama dama*) in seven studies, wild boar (*Sus*

scrofa) in six studies, and reindeer (*Rangifer tarandus*) in four studies.

In 29 of the studies of wild ungulates, the dominant species (or at least one of the co-dominant species) had formerly been introduced or re-introduced to the study areas.

Studies of domestic ungulates examined grazing effects mainly of cattle (15 cases), sheep (3 cases) or mixed or unspecified livestock (14 cases). Unlike studies of wild ungulates, the studies of livestock had mostly been carried out in Europe (18 cases) rather than North America (8 cases).

Effects of ungulate herbivory on vegetation were reported in 135 of the 144 included studies, whereas effects on invertebrates were reported in only 23 studies.

Responses to herbivory differ across subgroups of vegetation

Our synthesis of the included studies showed that ungulate herbivory generally reduced understorey vegetation *abundance* (Fig. 5). A negative effect of herbivory was also seen in the abundance of several subgroups of vegetation, including woody understorey as a whole, tree saplings (height > 1.5 m; diameter at breast height < 5 cm), shrubs, and bryophytes (mosses and liverworts). In contrast, the abundance of tree seedlings (height < 1.5 m), forbs and graminoids (grasses, sedges and rushes) showed no significant response.

Among individual tree genera, abundances of *Quercus* (oak) and *Tsuga* (hemlock) saplings/seedlings responded negatively to herbivory, whereas we found no significant response in *Abies* (fir), *Betula* (birch), *Corylus* (hazel), *Fagus* (beech), *Fraxinus* (ash), *Pinus* (pine), *Populus* (poplar/aspen), *Sorbus* (e.g. rowan), *Tilia* (lime) and *Ulmus* (elm).

The *species richness* of understorey vegetation as a whole was not significantly affected by herbivory (Fig. 5). Among subgroups of vegetation, we found a positive effect on species richness in forbs and bryophytes, but a negative effect in saplings and in woody understorey as a whole. The species richness of shrubs and graminoids showed no significant response.

Many factors can modify the effects of herbivory

Many factors may have contributed to the large variability that we found among herbivory effects reported by different studies. We analysed several factors of this kind and found some of them to be important.

For instance, we found that the effects of herbivory on understorey vegetation as a whole depended on the *origin of the ungulate* (Fig. 6).

Fig. 4. Many studies have examined the effects of herbivory by white-tailed deer, a North American species. Like e.g. moose and roe deer, this species largely feeds by browsing on woody vegetation.
Photo: Raul654 / Creative Commons.

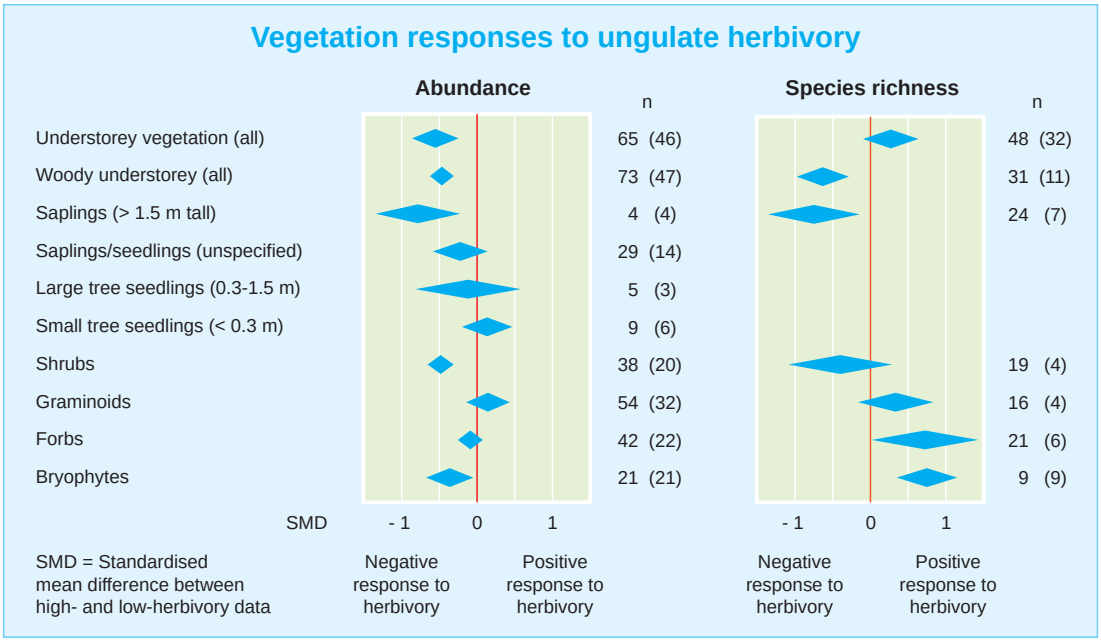

Fig. 5. Herbivory effects on the abundance and species richness of plants differ considerably across major subgroups of vegetation. Positions and widths of the diamond-shaped symbols indicate mean effects and 95% confidence intervals, respectively. Symbols spanning the red zero line represent non-significant effects. Sample sizes (n) refer to the number of individual comparisons, with the number of independent study sites given in brackets.

The response of understorey abundance was negative where the dominant ungulates were domestic (livestock) or introduced into the wild, but not where they were native or consisted of a mixture of native and introduced species.

In contrast, understorey species richness was favoured by grazing by domestic ungulates, but there was no significant effect of native or introduced wild ungulates.

We saw similar differences when we compared effects of ungulates with different *feeding strategies*. Understorey abundance was negatively affected by herbivory where the main herbivores were grazers (chiefly domestic ungulates) or intermediate grazers/browsers (e.g. *Cervus*, *Dama* or *Rangifer*), but not where they were browsers (e.g. *Alces*, *Capreolus* or *Odocoileus*). Understorey species richness was promoted by grazers but not by browsers or intermediate grazers/browsers.

We also found clear differences between effects of certain *kinds of intervention* (Fig. 6). In particular, while positive effects of herbivory on understorey species richness were usually seen in observational studies of sustained/abandoned/resumed livestock grazing, such effects were generally absent in studies where the density of ungulates (wild or domestic) had been regulated by means of fencing.

Fencing (exclosure or enclosure) studies of livestock tended to show a more positive response of understorey richness to herbivory than was observed in fencing studies of wild ungulates, but this difference was not statistically significant.

When separating study areas by *forest cover types*, we found that the understorey abundance responded negatively to herbivory only in temperate broadleaf/mixed forest and in stands dominated by conifers other than *Pinus*. In contrast, understorey species richness was favoured

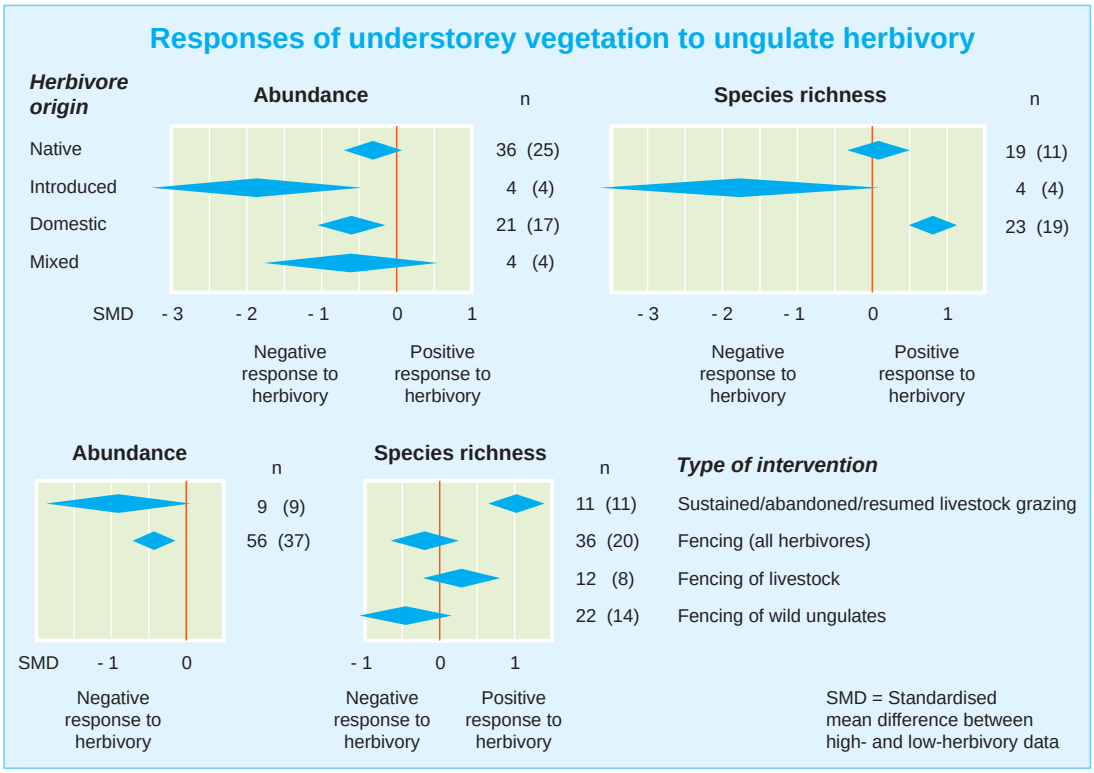

Fig. 6. Herbivore origin and type of intervention were identified as two of the more important modifiers of herbivory effects on understorey vegetation. See Fig. 5 for explanation of symbols.

by herbivory in boreal broadleaf/mixed forest and in stands that we categorised as 'poor-soil forest' (usually dominated by *Pinus*).

With increasing *duration* of herbivory manipulation, the abundance of forbs increased, whereas the species richness of saplings and of woody understorey as a whole decreased (Fig. 7). No significant impacts were detected on the abundance or species richness of other major groups of vegetation.

The *strength* of herbivory manipulation expressed as the difference in herbivore density or biomass between areas with high and low herbivory had relatively small impact on the abundance and species richness of vegetation (Fig. 7).

Somewhat clearer effects appeared when the strength of manipulation was expressed as 'herbivore years' (herbivore density × duration of manipulation). With an increase of the number of herbivore years, we found (1) decreasing abundance of understorey as a whole, of woody understorey and of shrubs; (2) increasing abundance of graminoids; (3) a decrease of the richness of saplings; (4) an increase of the richness of forbs.

However, few of these relationships also appeared when the strength of manipulation was expressed as 'herbivore biomass years' (herbivore biomass × duration of manipulation) (Fig. 7).

With increasing *mean annual temperature*, ungulate herbivory had increasingly negative effects on the species richness of understorey as a whole, woody understorey and saplings. Similarly, with increasing *mean annual precipitation*,

herbivory had increasingly negative effects on the abundance of shrubs and on the species richness of saplings and understorey as a whole.

The negative influence of temperature was partly due to the positive response of understorey richness commonly reported in studies of sustained/abandoned/resumed livestock grazing, most of which were performed in cool, high-latitude parts of Europe.

Effects of herbivory manipulation depend on the context

Our review synthesised a large amount of data on how manipulation of ungulate herbivory affects forest biodiversity. The systematic review method enabled us to identify a relevant selection of well-designed studies with a minimum of bias and subjectivity.

Influences of duration and strength of intervention on herbivory effects

Fig. 7. This diagram indicates whether the duration or strength of herbivory manipulation influenced its impacts on the abundance or species richness of different groups of vegetation. Four measures of strength of manipulation were applied: (1) change of herbivore density (no. of animals/km²), (2) change of herbivore biomass (kg/km²), (3) change expressed as 'herbivore years' (herbivore density × duration of manipulation), and (4) change expressed as 'herbivore biomass years' (herbivore biomass × duration of manipulation). Significant influences are indicated with asterisks.

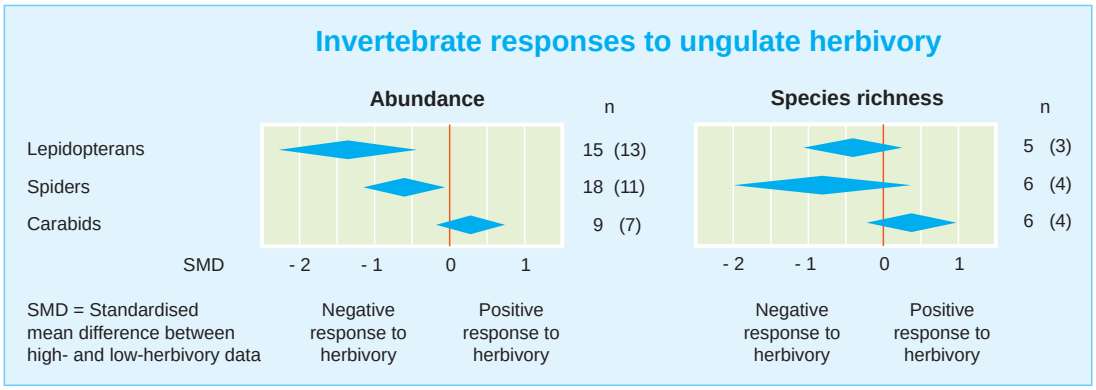

Fig. 8. The limited amount of data on invertebrates in studies included in this review restricted our ability to analyse herbivory effects on these taxa. The abundances of lepidopterans and spiders showed negative responses to herbivory, but their species richness did not respond significantly. For carabids there was a tendency for positive effects of herbivory on abundance and richness, but these effects were not significant. See Fig. 5 for explanation of symbols.

Taken together, the body of evidence confirms that manipulation of grazing/browsing pressure is often highly influential in terms of effects on tree regeneration and on the abundance, diversity and composition of plants and invertebrates.

A major finding of our review was that the context (climate, forest type, management history and herbivore identity) profoundly affects the impacts of ungulate herbivory on biodiversity.

Implications for management

Our results show that grazing/browsing reduces both abundance and species richness of the woody understorey as a whole and, in particular, of saplings. This has clear implications for the density and composition of overstorey trees. The fact that there were no significant effects of herbivory on the abundance of small seedlings suggests that tree regeneration generally becomes sensitive to herbivory only when trees have grown to sapling size. Often the important management issue is recruitment into the tree layer; effects on sapling abundance are thus critical.

Further, our results demonstrate that ungulate herbivory does not generally pose a risk for eradication of plant species from the herbaceous layer. Importantly, they also suggest that understorey vegetation is more likely to be affected by exposure to abundant introduced deer or livestock as compared to native ungulates. There was some evidence that livestock grazing can increase understorey species richness, but such effects may take many years to develop.

Overall, the findings suggest that manipulations designed to reduce herbivory in areas with high ungulate abundance could be used to encourage regeneration of certain tree species without concerns about reducing the diversity of herbaceous understorey or invertebrate communities. Plans to (re-)introduce or increase the abundance of ungulates, however, need to carefully consider potential undesirable outcomes on tree regeneration, understorey vegetation, and abundance of lepidopterans and spiders. This is especially the case if the manipulations will involve non-native ungulates or livestock.

The body of evidence that we present is mainly useful as a documentation of effects of high herbivore pressure. It is less suitable for identifying conservation values or targets for which ungulate herbivory is *necessary*. Nonetheless, our results suggest that conservation management based on livestock in forests should seek to opti-

mise the positive impacts of grazing on herbaceous plant richness while at least occasionally allowing tree saplings to reach maturity. The context-dependence demonstrated by our review further suggests that the balance between these two targets should be specified on a site-by-site basis.

Implications for further research

Prevailing designs of studies of ungulate herbivory have at least two major limitations.

First, since the mid-20th century, exclosure-based experiments have formed a standard that was most welcome when it was introduced. However, heavy reliance on such experiments can create a biased picture that emphasises visibly 'damaged' sites and a radical form of manipulation (complete removal of ungulates). The majority of studies in our review compared plots inside and outside exclosures in areas subject to intensive herbivory (typically this is what motivated the study in the first place). Thus, our results mainly relate to substantial, permanent declines in grazing/browsing pressure. To inform more nuanced approaches to herbivory management it would be useful to have more studies that examine responses along a gradient of grazing/browsing intensity, including seasonal grazing and both upward and downward manipulation of herbivory. Further, it would be useful to examine the influence of varying herbivory separately for different forest types because, in terms of carrying capacity, a given density of ungulates could be considered low in one ecosystem but excessively high in another.

Secondly, most studies that met our inclusion criteria were of relatively short duration (median of 6 years), although effects of herbivory manipulation can be expected to vary substantially over time. We thus emphasise the importance of maintaining studies of herbivory manipulation in the long term, and we call for analyses of all currently available results that cover at least 20 years.

How this review was conducted

This systematic review was initiated and financed by the Mistra Council for Evidence-Based Environmental Management (EviEM). The review was conducted by a specially appointed team of researchers chaired by Bengt Gunnar Jonsson, professor of ecology at Mid Sweden University in Sundsvall, Sweden. The main part of the work was carried out by Claes Bernes, Asko Lõhmus, Ellen Macdonald and Biljana Macura.

Fig. 9. The review team in November 2016. From left: Bengt Gunnar Jonsson, Jörg Müller, Asko Lõhmus, Ellen Macdonald, Jennie Sandström, Kaisa Junninen, Claes Bernes, Biljana Macura. Photo: Steningevik.

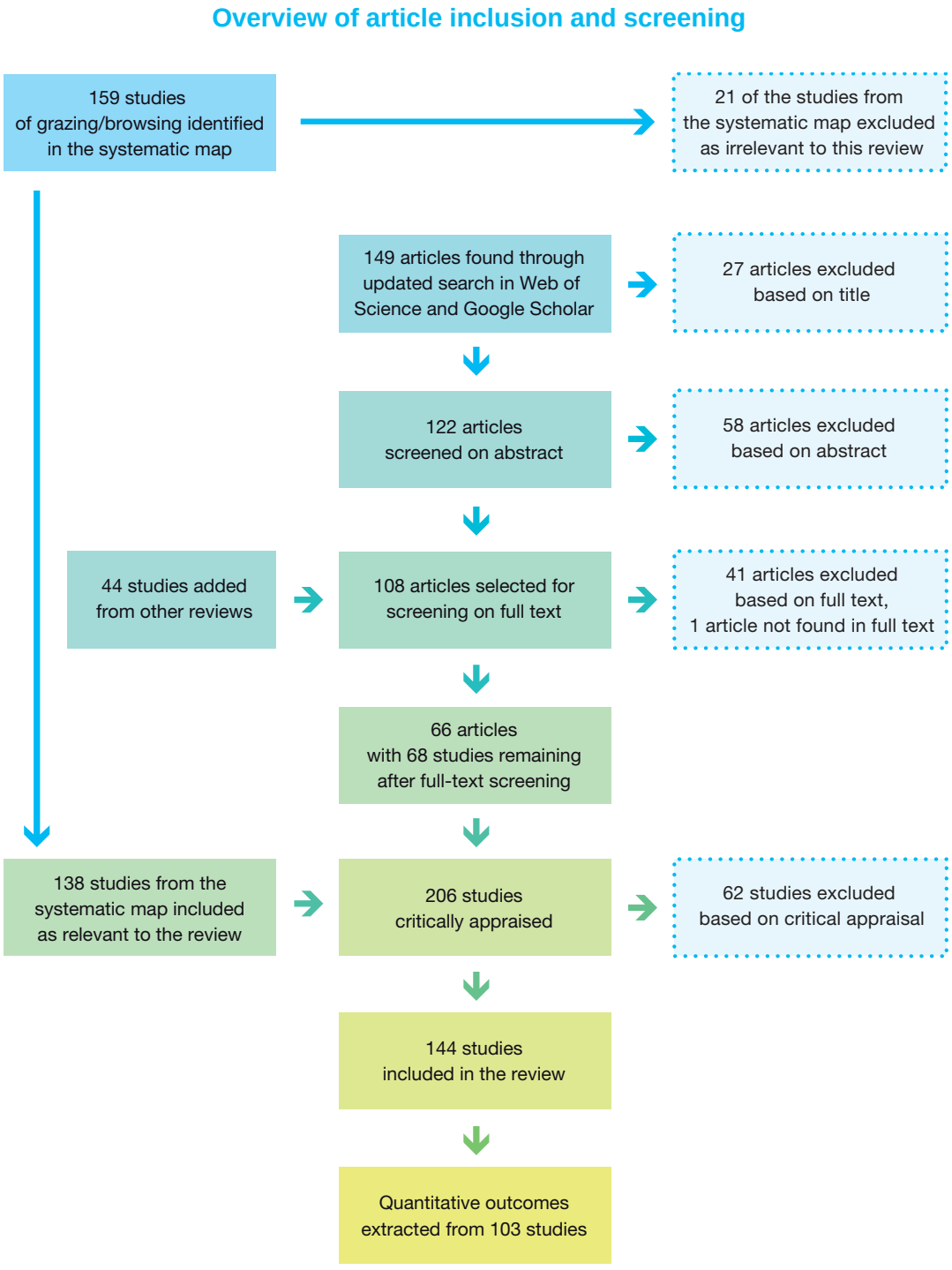

Fig. 10. About two thirds of the studies in this review were included from a systematic map of biodiversity effects of various forms of active forest management. The other studies were found through an updated search for literature in Web of Science, Google Scholar and bibliographies of existing reviews.

In 2015, the review team published a *systematic map* of the available evidence on effects of different forms of active management that could be used to conserve or restore biodiversity in forest set-asides (EviEM SR6). A systematic map provides an overview of the scope and focus of existing studies of a certain topic, but it does not summarise or synthesise the findings of the studies.

Based on the systematic map, we identified manipulation of mammalian herbivory as a topic with a sufficient number of studies for a full systematic review. Stakeholders with an interest in management of protected forests were invited to suggest modifications of the scope and focus of the review. The final design of the review was established in detail in a protocol that was published in September 2016.

Studies included in the systematic review were mainly selected from the systematic map. Additional studies were identified through updated searches online and in bibliographies of existing literature reviews (Fig. 10). While some of the studies were made in protected areas, we also considered studies performed in production forest.

We found a total of 206 relevant studies, but studies considered to have low or unclear validity were excluded from the review (Fig. 10). The most common reasons for exclusion were lack of replication and presence of confounding factors.

The vast majority of included articles were written in English, but four were written in Finnish, three in German and two in Swedish. Nearly all of the articles were published in peer-reviewed journals, but six were found in 'grey literature' (e.g. reports issued by national or local authorities, consultants etc.).

Most of the articles were relatively recent – only 19 of them were published earlier than 2000.

EviEM

The Mistra Council for Evidence-Based Environmental Management (EviEM) strives to ensure that environmental management in Sweden is informed by the best possible scientific evidence. Through systematic reviews of relevant research, we aim to improve the basis for decisions in environmental policy. Funded by the Swedish Foundation for Strategic Environmental Research (Mistra) and hosted by Stockholm Environment Institute, EviEM is financially and politically independent.

We extracted quantitative results from 103 of the studies. These data consisted of 1,317 comparisons across time and/or space of plants or invertebrates exposed to different levels of herbivory. Most of the data referred to the abundance (usually cover, stem density or biomass), height or species richness of plants, or to the abundance or species richness of invertebrates.

The meta-analyses that we finally conducted were aimed at determining the average effects of ungulate herbivory on different groups of plants or invertebrates. We also investigated to what extent herbivory effects on vegetation depended on the origin and feeding strategy of the ungulates, on forest cover type, climate and geographical location, and on the type, duration and intensity of the intervention that was intended to change the herbivory pressure.

Free access to full report

The full report on this systematic review is published in the *Environmental Evidence* journal (https://doi.org/10.1186/s13750-018-0125-3). The report is also available at EviEM's website (www.eviem.se). The report on the systematic map (SR6) that preceded the review can be found there too.

MISTRA EviEM
EVIDENCE-BASED ENVIRONMENTAL MANAGEMENT

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What are the possibilities of conserving or restoring valuable forest ecosystems by manipulating the populations of grazing and browsing animals? In the systematic review that is summarised here, we have investigated how changes of the grazing and browsing pressure by game and livestock affect forest plants and invertebrates.

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EviEM conducts systematic reviews of environmental issues identified as important by public agencies and other stakeholders. These provide an overall assessment of the state of scientific knowledge and help to improve the basis for environmental decision-making in Sweden.

Mistra EviEM
Stockholm Environment Institute
Box 24218, SE-104 51 Stockholm, Sweden

Visit: Linnégatan 87D, SE-115 23 Stockholm, Sweden
E-mail: info@eviem.se
Twitter: @MistraEviEM