

SYSTEMATIC REVIEW

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Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review

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Abstract

Background: Livestock grazing and 'overabundance' of large wild herbivores in forested areas have long been perceived as conflicting with the aims of both silviculture and forest conservation; however, certain kinds of herbivory can help to maintain habitat values in forest ecosystems. Management of mammalian herbivory in protected forests can, therefore, be a critical tool for biodiversity conservation. The primary aim of this systematic review 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.

Methods: 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. Non-intervention or alternative levels of intervention were used as comparators. Relevant outcomes included abundance, diversity and composition of plants and invertebrates, tree regeneration, and performance of focal/target species. Studies were mainly selected from a recent systematic map of the evidence on biodiversity effects of forest management relevant to protected areas. Additional studies were identified through updated searches online and in bibliographies of existing reviews. Relevant studies were critically appraised, and studies with low or unclear validity were excluded from the review. Quantitative outcomes were extracted from 103 articles, and summary effect sizes were derived by meta-analysis.

Results: 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 (or enclosure) of wild and/or domestic ungulates by fencing. Other studies examined culling of wild ungulates or compared forests long grazed by livestock to ungrazed forests. Effects on vegetation and invertebrates were reported in 135 and 23 of the studies, respectively. We found negative responses to herbivory in the abundance of understorey vegetation as a whole, woody understorey and bryophytes, and also in the species richness of woody understorey vegetation, whereas the richness of forbs and bryophytes responded positively. Several effects depended on ungulate origins: Understorey abundance responded negatively to livestock and to ungulates introduced into the wild, but not to native ones. In contrast, understorey species richness responded positively to livestock but not to wild ungulates. The duration and intensity of herbivory had few significant effects on vegetation—exceptions included woody understorey abundance

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and richness, which decreased with increasing duration and intensity, respectively. Among invertebrates we found negative responses to herbivory in the abundance of lepidopterans and spiders, but no significant effects on species richness.

Conclusions: Our review revealed a large body of high-validity experimental studies on impacts of ungulate herbivory in forests. This evidence confirmed that manipulation of such herbivory is often highly influential on tree regeneration and on the abundance, diversity and composition of understorey vegetation. Nevertheless, 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.

Keywords: Biodiversity, Deer, Forest conservation, Forest restoration, Forest set-aside, Herbivory, Livestock, Natural regeneration, Silvopastoral system, Wood-pasture

Background

Most forest regions host large herbivores as part of their native fauna, and these animals have an important influence on forest structure, composition and biodiversity [1–3]. Herbivores regulate tree regeneration, growth and survival; this, in turn, affects forest structural heterogeneity and regulates understorey plant communities [2, 4–8]. Large herbivores further filter understorey assemblages through preferential consumption of certain species, at the same time regulating competition among plants [9–13]. The influence of large herbivores extends to other biotic groups through effects on forest structure and composition of forest plant communities, but there are also direct impacts, such as trampling, faecal aggregations, and reduction of plant forage [14–17]. In parallel with broad-scale changes in herbivore populations, local effects can cascade to regional trends in biodiversity [18] and include development of new, relatively stable alternative states of some ecosystems [5, 19, 20]. Thus, herbivory is highly important for the maintenance of forest habitat values, including structural and compositional heterogeneity, as well as biodiversity [12, 21–23].

In many forest regions, human activities have greatly influenced the abundance and species composition of large mammalian herbivores. Such activities include the introduction of livestock grazing, introductions and regulation of game species, removal of top predators, and provision of supplementary forage [1, 5, 19]. They have, in turn, led to changes in the disturbance regime of these forests, sometimes resulting in either very high or very low ungulate herbivory pressure. At either extreme the intermediate disturbance hypothesis predicts reductions in biodiversity [24].

‘Overabundance’ of native wild herbivores has frequently been identified as a major challenge for forest regeneration and biodiversity conservation [1, 3, 5, 19], and livestock grazing too is often perceived as being in conflict with the aims of both silviculture and forest conservation [5, 25–27]. Through competition, additionally, livestock presence can limit habitat use by native

ungulates [28], thus potentially changing local herbivory regimes.

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 [29, 30], and the re-introduction of plains bison to Banff National Park in Canada was partially motivated by the recognition of their importance in maintaining habitat heterogeneity necessary to conserve biodiversity in the park [31]. Further, managed livestock grazing has been used to restore ecosystems that have become degraded due to a lack of wildfire [32], and has also been considered beneficial by improving nutrient cycling, controlling ground vegetation that competes with trees, and reducing fire risks [4].

Management of mammalian herbivory in protected areas can, therefore, be a critical tool for biodiversity conservation [8, 30, 33]. This can be especially true in forest set-asides, in which the current abundance and composition of mammal assemblages is often influenced by past management or by the isolated nature of protected areas. Several reviews of the impacts of herbivores on forests have already been published (e.g. [2, 3, 6, 7, 10, 11, 13, 14, 16]). Two of these used a systematic approach and included meta-analyses [10, 14], but the others were mainly narrative. Most of the reviews focused on effects of overabundance of specific herbivores, and they generally did not restrict themselves to studies where herbivory had been manipulated. There is still a shortage of quantitative assessments of the effects of grazing and browsing on biodiversity, especially across a range of herbivore abundances [5] and for different types of herbivore. Consequently, we still lack sufficient evidence to make informed decisions on regulation of wild herbivores or livestock to meet specific conservation targets in protected forests. This task is further complicated by the fact that active regulation of mammalian herbivores in protected areas, whether that be introduction of livestock grazing or control of populations of native species, can be

socially controversial (e.g. [20]). To navigate through the range of conceivable interventions, conservation managers must have explicit knowledge on the impacts of grazing and browsing on biodiversity.

There is obviously a need for an overview of the scientific evidence underlying different management options that could be used to meet biodiversity objectives in protected forests. To address this need, expressed not least by stakeholders in Sweden, we recently published a systematic map focused on the effects of active management on biodiversity in forests set aside for conservation or restoration [34]. We drew on studies conducted in forest set-asides and in forests under commercial management, but included only interventions that would be considered appropriate for use in protected areas to meet conservation objectives. Based on the systematic map, the impact of mammalian herbivory (chiefly grazing and browsing but also trampling and deposition of faeces) was identified as a topic with a sufficient number of studies to warrant a full systematic review. The topic was also considered important for stakeholders in Sweden and beyond. We subsequently published a protocol for this systematic review [35], focusing on wild ungulate and livestock impacts on vegetation and invertebrates in temperate and boreal forests. The present article reports the findings of the review.

Objective of the review

The broad aim of our systematic 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 deer and other wild ungulates, and also on studies of forest grazing by livestock. Our focus was on examining how the diversity of vegetation (understorey plants and lichens) and invertebrates is affected by manipulation of the grazing/browsing pressure by livestock or wild ungulates in temperate and boreal forests. Plants within herbivore reach are obviously both directly and indirectly affected by herbivory, and the structural diversity of vegetation is an important aspect of habitat value and thus of conservation value in itself. Invertebrates were included as a highly diverse group that is directly dependent on vegetation structure; further, Foster et al. [14] identified them as being particularly sensitive to mammalian herbivory. Both plants and invertebrates also include a number of threatened species.

Primary question: *What are the impacts of manipulating the pressure of grazing and browsing by livestock or wild ungulates on vegetation and invertebrates in temperate and boreal forests?*

Components of the primary question:

<i>Population</i>	Temperate and boreal forests
<i>Intervention</i>	Manipulation of the pressure of grazing and browsing by livestock or wild ungulates
<i>Comparator</i>	No manipulation of grazing/browsing pressure, or alternative strengths of manipulation (grazing/browsing pressure controlled at different levels)
<i>Outcomes</i>	Abundance, diversity and composition of vegetation and/or invertebrates Tree regeneration Performance (e.g. growth, reproduction) of target species (individual plant or invertebrate species that the intervention was intended to benefit or control).

In addition to examining the impacts of presence vs. absence of herbivory manipulation on forest structure, tree regeneration, understorey vegetation communities and invertebrate assemblages, our review addressed the following specific secondary 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, browser) of the main herbivores?
- How do the impacts of herbivory manipulation vary with the geographical context and habitat?

Methods

The design of this systematic review was established in detail in a peer-reviewed protocol [35]. It follows the guidelines for systematic reviews and evidence synthesis issued by the Collaboration for Environmental Evidence [36]. The scope and focus of the review was established in cooperation with stakeholders, primarily in Sweden. Before peer review, revision and final publication of the protocol, a draft version was open for public review at the website of the Mistra Council for Evidence-Based Environmental Management (EviEM) in March 2016. Comments were received from scientists, environmental managers and other stakeholders, and the draft was revised accordingly.

Search strategy

Most of the evidence examined in this systematic review was identified when we conducted systematic mapping of biodiversity impacts of active management relevant to forest set-asides [34]. The systematic map was based on literature searches using 13 publication databases, two

search engines, 24 specialist websites and 10 literature reviews. The majority of the literature searches were performed in May–August 2014, with an update in March 2015. About one-fifth of the studies included in the map reported on grazing/browsing effects and were therefore potentially relevant to this review.

In order to identify more recently published literature on effects of herbivory, we performed an additional search update in late April and early May 2016 using the following search terms:

<i>Subject</i>	forest*, woodland*, “wood* pasture*”, “wood* meadow*”
<i>Forest type</i>	boreal, boreonemoral, hemiboreal, nemoral, temperate, conifer*, deciduous, broadlea*, “mixed forest”, spruce, “Scots pine”, birch, aspen, beech, “ <i>Quercus robur</i> ”, Swed*
<i>Intervention</i>	graz*, brows*, fenc*, exclos*
<i>Outcomes</i>	*diversity, [species AND (richness OR focal OR target OR keystone OR umbrella OR red-list* OR threatened OR endangered OR rare)], “species density”, “number of species”, indicator*, abundance, habitat*.

These search terms were a subset of the search string used for the systematic map [34], in that ‘intervention’ terms were restricted to those designed to capture literature on manipulation of grazing or browsing. The terms and substrings within each category (‘subject’, ‘forest type’, ‘intervention’ and ‘outcomes’) were combined using the Boolean operator ‘OR’. The four categories were then combined using the Boolean operator ‘AND’. An asterisk (*) is a ‘wildcard’ that represents any group of characters, including no character.

The updated search for articles on herbivory effects covered peer-reviewed and grey literature published in 2014 or later and was made using Web of Science and Google Scholar. In the latter case, the first 200 hits (sorted by relevance) were examined for useful articles. No language or document type restrictions were applied.

Additionally, we made a comprehensive search for other potentially relevant articles by examining the bibliographies of existing reviews of mammalian herbivory in forests. One reason for this effort was that our original and updated literature searches of publication databases used a set of search terms focusing on forests with tree species commonly occurring in Sweden (the ‘forest type’ terms listed above). This was intended to keep the amount of evidence at a manageable level—without the ‘forest type’ terms, the amount of literature to be

screened for the systematic map would have increased about fourfold. In the present review, however, we aimed to be more inclusive. By searching in review bibliographies we attempted to identify additional relevant literature on ungulate herbivory in temperate and boreal forests that might have been missed by our searches of publication databases. A detailed description of our searches for literature is available in Additional file 1.

Article screening and study eligibility criteria

Articles identified through the updated search in Web of Science and Google Scholar were evaluated for inclusion at three successive levels. First, they were assessed by title. Next, each article found to be potentially relevant on the basis of title was judged for inclusion on the basis of abstract. Finally, each article found to be potentially relevant on the basis of abstract was judged for inclusion based on the full text. At this stage, we also assessed articles found in review bibliographies.

The screening of articles from the search update could be seen as a continuation of the screening conducted for the systematic map, during which detailed, multi-level consistency checking was performed. The work was carried out by a reviewer (CB) who participated in the screening of articles for the systematic map, and who was therefore well acquainted with the relevant literature and with the criteria for inclusion. Articles identified by the reviewer as potentially useful (or doubtful) based on full text were then assessed by a second reviewer, and none of the reviewers assessed studies authored by themselves. Final decisions on whether to include doubtful cases were taken by the review team as a whole. A list of articles rejected on the basis of full-text assessment is provided in Additional file 2 together with the reasons for exclusion.

In order to be included, each article had to pass each of the following criteria (based on those used for the systematic map [34] but more restrictive regarding interventions and outcomes):

- *Relevant subjects* Forests in the boreal or temperate vegetation zones. Any habitat with a tree layer was regarded as forest. This means that studies of e.g. wooded meadows and urban woodlands could be included, but we excluded studies of areas that did not have an established tree layer when manipulation of ungulate herbivory started (e.g. due to recent clearcutting or intensive burning). As an approximation of the boreal and temperate vegetation zones we used the cold Köppen–Geiger climate zones (the D zones) and some of the temperate ones (Cfb, Cfc and Csb), as defined by Peel et al. [37]. The other temperate Köppen–Geiger climate

zones are often referred to as subtropical and were therefore considered to fall outside the scope of this review. Nevertheless, forest stands dominated by ponderosa pine (*Pinus ponderosa*) were considered relevant even if located outside the climate zones mentioned above. These forests constitute a well-studied North American ecosystem type that shares several characteristics and management issues with the pine forests in boreal and temperate regions, especially in Europe [38].

- *Relevant types of intervention* Manipulation of ungulate herbivory, e.g. by fencing or by introduction or culling of ungulates. Studies of areas where herbivory varied for reasons other than direct manipulation (e.g. because of natural differences in the availability or accessibility of food) were not included. Nor did we include studies of simulated herbivory if the simulation merely consisted of artificial removal of vegetation.
- *Relevant type of comparator* Non-intervention or alternative levels of intervention. Both temporal and spatial comparisons of how manipulation of ungulate herbivory affects biodiversity were considered to be relevant. This means that we included both 'BA' (Before/After) studies, i.e. comparisons of the same site prior to and following an intervention, and 'CI' (Control/Impact) studies, i.e. comparisons of treated and untreated sites (or sites that had been subject to different kinds of treatment). Studies combining these types of comparison, i.e. those with a 'BACI' (Before/After/Control/Impact) design, were also included.
- *Relevant types of outcome* Abundance, diversity or composition of vegetation (vascular plants, bryophytes and lichens) and/or invertebrates; tree regeneration (seedlings and saplings); performance (e.g. growth, reproduction) of target species (individual plant or invertebrate species that the intervention was intended to benefit or control).
- *Relevant type of study* Primary field studies. Based on this criterion, we excluded e.g. review papers, modelling studies and policy discussions.
- *Language* Full text written in English, French, German, Danish, Norwegian, Swedish, Finnish, Estonian or Russian.

Study validity assessment

Articles that passed the relevance criteria described above were subject to critical appraisal. This appraisal was carried out on a study-by-study basis rather than article by article. If a single article reported on more than one investigation or experiment, these were regarded as

separate studies if they had different designs (e.g. different experimental set-ups).

Based on assessments of their clarity and susceptibility to bias, studies were categorised as having high, medium, low or unclear validity (with regard to our review question). A study was excluded from the review due to low validity if any of the following factors applied:

- No true replication.
- Intervention and comparator sites not well-matched.
- Severely confounding factors present.

Confounding factors included conditions that differed between intervention and control sites, and additional interventions that co-varied with the manipulation of grazing/browsing pressure. Historically, for example, wood-pastures were often used for multiple purposes—there, grazing could be combined with e.g. mowing, acorn collecting, litter raking and field crop cultivation [39]. However, present-day reserve management typically requires separate consideration of each intervention; therefore, studies of such combined activities (even if historically relevant) were excluded unless the main effect of grazing could be distinguished.

We also excluded studies that were unclear to such an extent that their validity could not be judged, for instance due to absence of key information on study design. More specifically, we categorised a study as having unclear validity if any of the following factors applied:

- Methodological description insufficient for assessment of study design.
- Outcomes difficult to interpret (e.g. since data from forested and treeless study sites were pooled).
- Intervention difficult to interpret (e.g. not clear whether the herbivory of ungulates actually was manipulated).

A study that was not excluded due to low or unclear validity was considered to have medium validity if any of the following factors applied:

- Location of study plots potentially biased (e.g. due to large habitat variation).
- BA study design (not CI or BACI).
- No quantitative data on grazing/browsing pressure.
- Experimental set-up excluded small mammals as well as ungulates.

If none of the above factors applied, the study was considered to have high validity.

The last of the criteria mentioned above was not included in the review protocol [35]. It was subsequently

added since some studies used fine-meshed fences that excluded not only ungulates but also locally abundant smaller mammals such as hares and rodents; thus it was impossible in these cases to single out specific effects of ungulate herbivory. One of the validity criteria listed in the protocol, “No useful data on variance or sample sizes”, was discarded, since this is an issue of reporting rather than of study validity, and outcome variability and sample sizes may be available from study authors even where such data are not published.

All studies were assessed by at least two reviewers, and reviewers did not assess studies authored by themselves. Final rulings on how to classify doubtful study categories were made by the review team as a whole. A list of studies excluded on the basis of validity assessment is provided in Additional file 3 together with the reasons for exclusion.

Data extraction strategy

Outcome means, estimates of precision or variability (standard deviations, standard errors, confidence intervals) and sample sizes were extracted from tables and graphs, using image analysis software (WebPlotDigitizer) when necessary. Where outcomes were available for several different years after intervention, we extracted data for the most recent year only.

Based on judgements of scientific relevance, stakeholder interests and availability of data, we decided to focus the extraction of outcomes for meta-analysis on the following response variables:

Vegetation:

- Abundance and species richness of understorey vegetation as a whole.
- Abundance and species richness of major groups of understorey plants (mainly tree seedlings and saplings, shrubs, woody understorey vegetation as a whole, graminoids, forbs, bryophytes, and native vs. exotic species).
- Abundance and survival of seedlings and saplings of certain tree genera of particular relevance to the forest types we focused on (*Abies*, *Betula*, *Corylus*, *Fagus*, *Fraxinus*, *Pinus*, *Populus*, *Quercus*, *Sorbus*, *Thuja*, *Tilia*, *Tsuga*, *Ulmus*). These genera include e.g. dominants of supposedly herbivory-sensitive forest ecosystems [5], threatened species, and species of cultural significance.
- Height (or height growth) of tree seedlings and saplings (of any species).
- Abundance of certain frequently studied plant species that are either common in regions covered by this review (*Calluna vulgaris*, *Deschampsia flexuosa*,

Empetrum nigrum, *Maianthemum canadense*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*), invasive (*Alliaria petiolata*, *Microstegium vimineum*), or of interest for conservation (*Trillium* spp.).

- Flowering and other measures of sexual reproduction (in any plant species).

Invertebrates:

- Species richness and total abundance of spiders, carabids and lepidopterans.

Definitions of ‘understorey’ and ‘tree seedlings/saplings’ varied from article to article. In this review, we chose to categorise vegetation as ‘understorey vegetation as a whole’ not only when authors reported it as ‘understorey’ but also when they described it as ‘field/herb-layer vegetation’, ‘vascular plants’ or ‘non-woody plants’ (in some cases also when they reported it as ‘ground-layer vegetation’). We defined ‘tree seedlings’ as trees shorter than 1.5 m and ‘saplings’ as trees taller than 1.5 m with a diameter at breast height (dbh) less than 5 cm. Due to the limited amount of specific data on seedlings, our analyses of herbivory effects on young trees were generally restricted to saplings, among which we included data on saplings of unspecified size and sizes that agreed only partially with our own definition of saplings. Nevertheless, we also conducted analyses of seedlings, separating them into small (<0.3 m height) and large individuals (0.3–1.5 m height) because the former often escape ungulate consumption and their establishment and survival may be favoured by the increase of light that accompanies removal by herbivores of taller vegetation (e.g. [8, 40]). Vegetation described by study authors as ‘herbs’ was categorised by us as ‘forbs’ if it was clear that the authors were not referring to herbaceous plants in general (i.e., both graminoids and forbs).

The initial selection of outcomes to be extracted from an article was made by one reviewer. A second reviewer reassessed this selection and performed the actual data extraction, and a large subset of the extracted data was then double-checked by a third reviewer.

In some cases, we asked study authors to supply outcomes in digital format. This was done where relevant findings were published in graphs from which it was difficult to extract data accurately enough, when it was known or assumed that considerable amounts of relevant but unpublished data were available in addition to the published results, and where outcomes were presented in a way that impeded inclusion in meta-analyses. The latter cases included studies where outcomes were reported as medians and percentiles rather than means and standard errors, or where they were based on partly

pseudoreplicated data (in the sense that reported standard errors did not refer to the variability of true replicate means but to the variability of subsamples both within and across all true replicates). Where raw data were provided, summary statistics were calculated by us.

Each pair of BA or CI outcomes (and each quadruple of BACI outcomes) was recorded in a separate row of an Excel spreadsheet together with associated meta-data such as bibliographic information and potential effect modifiers (see next section). Extracted data records are available in Additional file 4.

Potential effect modifiers and reasons for heterogeneity

To the extent that data were available, the following potential effect modifiers were considered and recorded for studies included in this review:

- Geographical coordinates.
- Altitude.
- Mean annual temperature and precipitation.
- Forest cover type.
- Dominant tree species.
- Palatability of tree species subject to browsing.
- Mean age of forest stand.
- Forest density (e.g. overstorey canopy cover, basal area or stem density).
- Type of manipulation of herbivory (exclosures, enclosures, culling etc.)
- Herbivore species subject to manipulation.
- Herbivore origin (native/introduced/domestic).
- Extent of areas where herbivory was manipulated (e.g. size of herbivore exclosures).
- Grazing/browsing pressure (e.g. herbivore density).
- Duration of manipulation (or time elapsed from start of manipulation to final sampling).
- Conservation concern addressed by manipulation.
- Other interventions at study sites (harvesting, thinning, understorey removal, mowing, burning etc.)
- Size of sampling plots.
- Landscape aspects (such as degree of isolation).
- History of land use, herbivory and protection.

If geographical coordinates of study sites were not provided in an article, we recorded approximate coordinates based on published site names, maps or verbal descriptions of study locations (or coordinates provided in another article describing the same site). Data on mean annual temperature and precipitation for each study location were retrieved from the WorldClim database [41] using the coordinates of study sites.

Based on climate zones and dominant tree species, the forest cover type at study sites was assigned by us to one of six categories: Temperate broadleaf/mixed, boreal

broadleaf/mixed, poor-soil forest (usually dominated by *Pinus* spp.), richer-soil conifers (conifers other than *Pinus*), open woodland, and regenerating stands (age 5–20 years). The palatability of tree species was categorised as high, medium or low based on data from external sources. For each species we recorded a ‘best estimate’ of palatability based on a balanced assessment of data from the main sources, and also the highest estimate of palatability found in any of these sources (see Additional file 5).

Moreover, we transformed grazing/browsing pressure data given as *herbivore density* (number of ungulates per km²) to *herbivore biomass* (kg/km²) using information from external sources on the average metabolic body mass of various ungulate species (Additional file 6). We also derived two additional measures of the grazing/browsing pressure: *herbivore years* and *herbivore biomass years*, calculated as the duration (in years) of herbivore manipulation multiplied by herbivore density and herbivore biomass, respectively. In areas where grazing only occurred during part of the year, we prorated the herbivore density by multiplying the number of ungulates per km² during the grazing season by the fraction of the year covered by this season. Where the herbivore density and/or the duration of manipulation were reported as ranges or uncertain estimates, we used arithmetic means and conservative approximations, respectively. For instance, if the duration of manipulation was reported as ‘more than 15 years’, we used 16 years as an approximation.

Based on their feeding strategies we categorised ungulate species as grazers, intermediate grazers/browsers or browsers, mainly following Perez-Barberia et al. [42]. Otherwise, we relied entirely on the included studies for data on potential effect modifiers.

Data synthesis and presentation

Narrative synthesis methodology

All studies included in the review are listed and briefly described in a narrative table (Additional file 7) in which the following information is provided for each study:

- Full reference.
- Language of article.
- Study validity.
- Site ID(s).
- Location of study site(s).
- Characteristics of study site(s) (climate, forest type, land use history, landscape aspects).
- Type, duration and replication of herbivory manipulation.
- Conservation concern addressed by the manipulation.
- Other interventions in study site(s).

- Species and grazing/browsing pressure of dominant ungulate(s).
- Sizes and numbers of manipulation and sampling areas.
- Study design (BA/CI/BACI).
- No. of comparisons extracted for meta-analysis.
- Summary of findings (herbivory effects) as reported by study authors.

The findings summarised in the narrative table (Additional file 7, Column AO) include not only outcomes that we synthesised quantitatively ourselves, as described below, but also outcomes that could not be analysed in this way since they were reported too heterogeneously or by too few studies. The latter outcomes include (but are not restricted to) herbivory effects on lichens, vines, ferns, invertebrates other than lepidopterans, spiders or carabids, and single species other than the target tree and understorey plant species that we included in our meta-analyses.

Where published statistical analyses showed a significant interaction between herbivory manipulation and another factor, for example year or some other treatment, we noted whether the herbivory manipulation treatment was only significant within a given level of the other factor. In some such cases no post hoc tests were done to tease out the significance of the herbivory manipulation alone; in these cases we reported the results as given by the authors and indicated that there was no test of significance for the herbivory treatment alone.

A challenge in interpreting results of studies was when the design involved true replicates but it was clear, or we highly suspected, that the statistical analyses had involved pseudoreplication (subsamples treated as true replicates; see Additional file 7, Column AP).

Conversion and characterisation of outcomes used in quantitative synthesis

In preparation for quantitative analyses, we made a number of initial conversions and transformations of outcomes extracted from included studies. BACI outcomes were converted to CI by subtraction of data from sampling before intervention from those collected after intervention. Estimates of precision recorded as standard errors or confidence intervals were converted to standard deviations. In some cases, where study authors had published vegetation data employing plant categories more specific than those we used in our analyses, we combined different outcomes from the same plots through addition (e.g. aggregating separate abundance data on grasses and sedges to obtain the abundance of graminoids). Where the same response variable had been measured repeatedly in the same plots in a single year, we combined the

outcomes by averaging means and pooling standard deviations.

In some cases, the same response variable had been measured in several different plots at the same site (or set of sites); typically, this occurred when the plots were subject to different levels of ungulate herbivory or to various additional interventions, or if they were characterised by different soil types or other local conditions. In such cases, the outcomes could not be considered as independent of each other. All outcomes from a single site (or set of sites) were therefore given a unique site ID that was included in the analyses as a random factor (see below).

On the other hand, if a single study presented data on the same response variable from different sites (with true replication at each site, and with sites located more than 1 km apart and/or in stands with clearly different characteristics, such as coniferous vs. broadleaf forest), we regarded these data as independent, giving them different site IDs and including them in the analyses in the same way as outcomes from different studies.

Calculation of effect sizes

Standardised mean difference (SMD) effect sizes were derived for all outcomes using Hedges' *g* statistic (equations 4.19 and 4.22 in Borenstein et al. [43]). The effect sizes were based on the difference between the mean response at high(er) grazing/browsing pressure and the mean response at low (or no) pressure, divided by the pooled standard deviation. Positive effect sizes thus indicate that the response parameter was higher at high ungulate herbivory than at lower herbivory.

In a few studies of replicated pairs of high- and low-herbivory plots, authors reported outcomes for each such replicate without publishing overall means and variability. In these cases, we derived the latter data ourselves, normally by calculating means and standard deviations separately for high- and low-herbivory plots and then obtaining the SMD as the difference between these means divided by the pooled standard deviation.

Where we knew (based on published information or contacts with authors) or had reason to assume that published outcomes were based on partly pseudoreplicated data (see Data extraction strategy), we modified the calculation of effect sizes to avoid giving such outcomes undue influence on our results. First, standard errors were converted to standard deviations using the total number of subsamples as the sample size. SMDs (Hedges' *g* statistic) were also calculated using the total number of subsamples, but variances of SMDs were calculated using the number of true replicates in the first part of equation 4.20 in Borenstein et al. [43] and the number of subsamples in the second part of this equation. The same technique for calculating SMDs and their variances was

applied where we had averaged outcomes from repeated sampling in a single year (see above), since these outcomes could be regarded as temporally pseudoreplicated.

Meta-analyses

Meta-analyses of the impacts of ungulate herbivory on plants and invertebrates were carried out with the metafor package [44] within the R environment v. 3.4.0 [45]. We calculated summary effect sizes with random effects models, using restricted maximum likelihood to estimate heterogeneity and with site ID included as a random factor.

Initially, we analysed effects of high vs. low herbivory on the response variables listed under data extraction strategy (primarily the abundance or species richness of various taxonomic groups). Vegetation abundance was reported in several different ways in the literature (mainly as cover, density or biomass), but we usually combined these measures in our analyses. Data are presented in forest plots showing mean effect sizes and 95% confidence intervals, and in overviews comparing summary effect sizes from different analyses.

For vegetation data, we also performed subgroup analyses to estimate impacts of a number of categorical effect modifiers: herbivore origin, herbivore feeding strategy, type of intervention used to manipulate ungulate herbivory, forest cover type, and plant palatability.

Impacts of continuous effect modifiers were analysed by means of meta-regression, with vegetation abundance or richness as the dependent variable. Independent variables included intervention strength, duration of herbivory manipulation (time elapsed from start of manipulation to sampling of outcomes), mean annual temperature, mean annual precipitation, and latitude. The intervention strength was calculated as the difference between areas with high and low herbivory of any of the four measures of grazing/browsing pressure that we used (herbivore density, herbivore biomass, herbivore years or herbivore biomass years—see potential effect modifiers above).

Due to skewness of the data for mean annual precipitation, duration of manipulation, and all measures of intervention strength, we log-transformed those variables before analysis. We also calculated the correlations between all continuous effect modifiers included in our meta-regressions.

Analyses of species composition

Data on species composition are difficult to assess with conventional meta-analytical techniques. We divided studies that reported such data into two groups: studies that showed significant differences in species composition between areas exposed to high and low (or no

herbivory, and studies that showed no clear differences of that kind. This categorisation was mainly based on visual inspection of ordination diagrams (by study authors or ourselves)—only rarely had the authors used multivariate statistical analyses (e.g., PERMANOVA, MRPP, dbRDA) to test for significant differences in species composition. We then calculated means of reported effect modifiers (e.g. the duration of herbivory manipulation) for each of the two groups of studies and checked whether the means differed significantly between the groups.

Analyses of bias

Additional analyses were made to investigate whether our findings might be affected by bias caused by suboptimal study designs or by various statistical treatments carried out by study authors or ourselves. Such analyses were based on data on the abundance and species richness of understorey vegetation, since these were the response variables most frequently reported in studies included in the review.

- To check whether findings were dependent on study validity, we compared results for understorey vegetation based on high- and medium-validity studies.
- In studies based on fencing to exclude or enclose ungulates, we investigated the influence of the size of the manipulated area by performing separate analyses of data from exclosures/enclosures smaller versus larger than 0.1 ha.
- While we included some partly pseudoreplicated data in our analyses (see above), we also examined the consequences of excluding these outcomes entirely from the analyses.
- Where study authors reported outcomes from replicated plot pairs individually, without publishing overall means and variability, we normally calculated the SMD with the procedure described above. However, we also checked the consequences of using an alternative SMD calculated as the mean difference between individual plot pairs divided by the standard deviation of this mean. If within-pair differences are smaller than between-pair differences, larger SMDs will be found with the alternative method than with the one we normally used, and vice versa.

Finally, we tested for possible publication bias using funnel plots for the available data on understorey abundance and richness. Funnel plots are scatter plots of effect sizes against an estimate of precision, usually the standard error. However, funnel plots that combine SMDs and standard errors are susceptible to distortions that could be interpreted as signs of publication bias even where no

such bias is present [46]. As recommended by Zwetsloot et al. [46], we used the inverse square root of the sample size as a measure of precision in our funnel plots.

Results

Review descriptive statistics

Literature identification and screening

Our systematic map of biodiversity impacts of various forms of active forest management included a total of 812 studies [34]. Of these, 157 were listed as describing effects of grazing (or browsing) and were thus potentially eligible for inclusion in this review. When reassessing these studies, we concluded that two of them ([47] and [48]) actually consisted of two separate studies each. Another study was excluded since it had been erroneously categorised in the systematic map as an investigation of grazing/browsing effects. We also excluded five studies where the main herbivore was not an ungulate, four where study sites were not covered by a tree layer when the manipulation of herbivory was initiated, and 11 studies with outcomes that did not fulfil our eligibility criteria. This left 138 studies from the systematic map that we considered as relevant to this review (see Fig. 1). Excluded articles are listed in Additional file 2 together with the reason for exclusion.

The updated search for literature on effects of forest grazing/browsing returned 216 articles from Web of Science, 143 of which had not been found when we searched for literature for the systematic map (because they had been published more recently; see Additional file 1). In Google Scholar, we identified another six potentially useful articles that had not already been found. Title screening of the 149 new articles left 122 that we considered as potentially relevant. After screening on abstracts, 64 of these articles remained. At this stage of the process, we also introduced 44 potentially relevant articles that had been identified through examination of bibliographies in review articles. Consequently, a total of 108 articles were selected for full-text screening. After this screening, 66 articles remained, two of which reported on two separate studies (Fig. 1). Reasons for exclusion at full-text screening are provided in Additional file 2 and summarised in Table 1.

Critical appraisal of the 206 studies that had passed relevance screening led to the exclusion of 62 studies due to low or unclear validity (see Additional file 3 and narrative synthesis below). Consequently, 144 studies (described in 140 articles) were included in this review. The vast majority of articles (131) were written in English, but four were written in Finnish, three in German and two in Swedish. Nearly all of the articles (134) were published in peer-reviewed journals (*Forest Ecology and Management* being the journal most frequently represented, with 26 articles),

but six were found in grey literature. Most of the articles were relatively recent—the median year of publication was 2009, and only 19 of the articles were published earlier than 2000. The earliest articles that met our criteria for inclusion appeared in 1983 [49, 50].

Characteristics of included studies

Slightly more than half of the 144 studies included in the review were conducted in North America, with 64 being performed in the US and 11 in Canada. The other studies were mostly made in Europe (53)—with 13 in Sweden, 11 in Finland, nine in the UK, and six each in Germany and Norway—or in Australia/New Zealand (14). One study was performed in Argentina and one in Japan. 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. 2a). In terms of climatic conditions, the studies represented precipitation conditions found in the temperate and boreal regions relatively well, whereas low-temperature areas appeared to be understudied (Fig. 2b). Extensive parts of the latter areas are covered by tundra and therefore not relevant to our review, however.

Of the six forest cover types that we had defined, temperate broadleaf/mixed forest was by far the most frequently represented in our review, being covered by 80 studies (Table 2). Quantitative data on basal area, canopy cover or other measures of forest density were published in 62 of the 144 studies included in the review. In the 29 studies that provided estimates of basal area, averages ranged from 10.6 to 65.6 m²/ha, with a median of 31 m²/ha. Reported stand ages at the beginning of herbivory manipulation varied between 5 and more than 100 years, but quantitative age estimates were only available in 33 studies. In 23 other studies, forest stands were characterised as ‘mature’ or ‘old-growth’; the remaining 88 studies provided no information about the age of investigated stands.

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. In eight studies, fenced enclosures were used to keep ungulates at controlled densities lower and/or higher than the ambient mean. Two studies were based on simulated moose (*Alces alces*) browsing which involved clipping of vegetation and deposition of dung/urine. 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 livestock or reindeer to areas that were long ungrazed or where grazing was abandoned, or were Before-After studies in

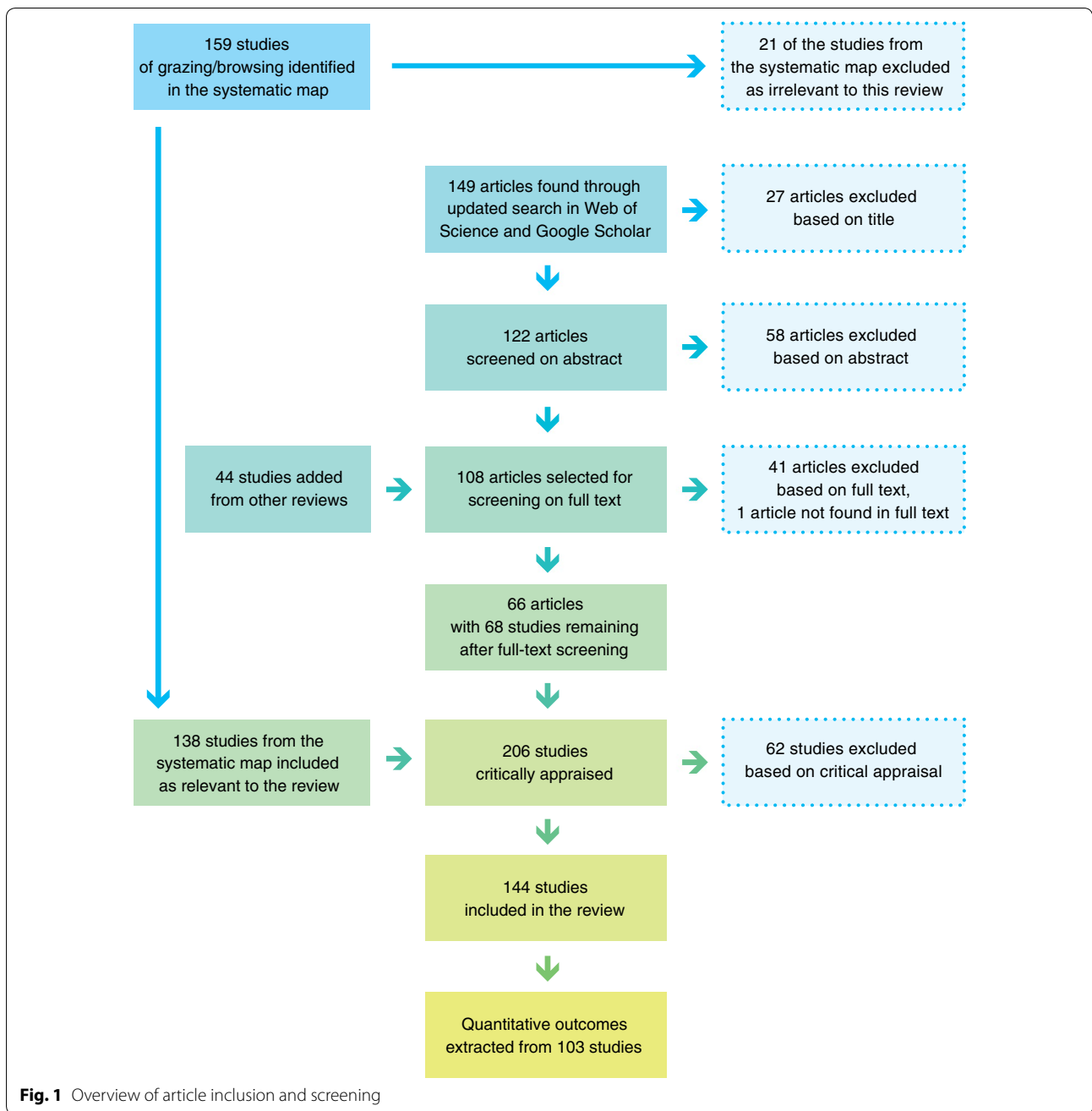


Fig. 1 Overview of article inclusion and screening

areas where livestock grazing was resumed), whereas six studies investigated effects of culling of wild ungulates. One study reported on effects of supplementary feeding of moose in unfenced areas. Nine studies combined two types of herbivory manipulation (in most cases exclusion and enclosure of ungulates).

Sizes of ungulate enclosures ranged from 0.5 m² to 2428 ha, with a median of 400 m², whereas enclosure sizes ranged from 0.6 to 2100 ha (median around 20 ha). In the sustained/abandoned/resumed grazing studies

the areas where livestock was kept ranged in size from 0.35 ha to 339 ha, with a median of ~10 ha.

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

Table 1 Reasons for exclusions at full-text screening of articles from the search update

Reason for exclusion	No. of articles
Not a study of forests, woodlands or other terrestrial habitats with a tree layer	8
Not a study made in boreal or temperate vegetation zones	9
Not a field study	2
Not a study of manipulation of herbivory	15
Not a study of ungulate herbivory	1
No useful comparator data	3
No outcomes relevant to this review	4
Redundant (relevant outcomes also reported elsewhere)	1
Full text not found	1

Two of the 42 excluded articles appear more than once in the table, since they were excluded for more than one reason

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. Of these studies, eight had been conducted in New Zealand and six on Canadian islands historically lacking ungulates, whereas the others had been performed in parts of Europe, North America or South America where exotic ungulates had been added to the fauna (9 studies) or in parts of North America where elk or white-tailed deer had been re-introduced (6 studies).

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).

Quantitative data on the grazing/browsing pressure were available for 91 of the studies in the review. In 84 cases, these data consisted of observations or estimates of herbivore densities (Table 3), whereas seven studies reported other measures of grazing/browsing pressure (usually densities of faecal pellets) without attempting to convert such data to animal densities.

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. In 14 studies, data were presented on effects of herbivory on both vegetation and invertebrates.

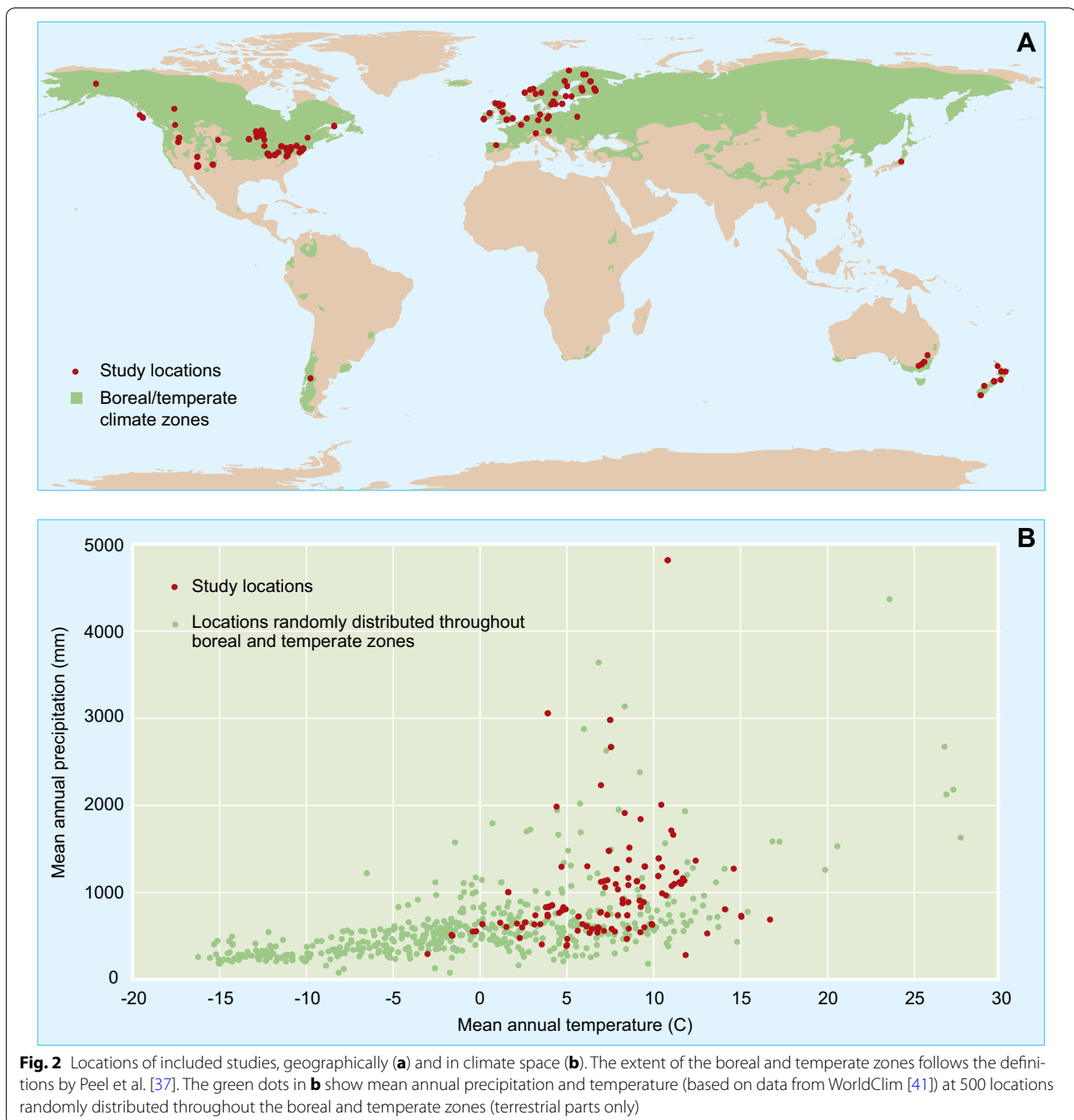
Narrative synthesis including study validity assessment

Of the 62 studies excluded based on our critical appraisal (see above), 52 were considered to have low validity, while the other 10 were considered to have unclear validity (see Additional file 3). The main reasons for exclusion were lack of true replication (35 studies) and presence of severely confounding factors (19 studies). Of the 144 studies included in the review, 81 were categorised as having high validity. The other 63 studies were considered to have medium validity, most commonly because no quantitative information was provided on the grazing/browsing pressure (54 cases).

For all of the included studies, we recorded descriptions of the study locations in the narrative table (Additional file 7). However, in many cases authors reported little data on the settings of their studies. For over half of the studies there was no information on the landscape context for the study area (Additional file 7, Column AC) although this is no doubt an important factor influencing ungulate herbivory pressure. Articles that did report such information show wide variation, with studies conducted in intact forest landscapes, forest patches within heterogeneous landscapes, isolated forest fragments (often surrounded by agriculture), suburban parks and on islands.

In nearly half of the studies some other intervention had been applied in addition to manipulation of ungulate herbivory; the most common types were harvesting (partial harvesting, thinning, gap felling), prescribed burning, transplantation of desired plant species or removal of invasive plants. In a few studies, the herbivore density in the 'high herbivory' treatment was regulated downward somewhat by hunting or hormonal birth control. Among the conservation concerns that motivated the manipulation of herbivory, the most common were tree regeneration, understory plant diversity, invasive plant species, target plant species (forest specialists or important berry species), and arthropod or bird biodiversity (Additional file 7, Column AK).

The vast majority of studies involved a Control/Impact (CI) design, while 14 were Before/After/Control/Impact (BACI) studies and only six were Before/After (BA) studies (Additional file 7, Column AL). A very common experimental set-up for the CI studies was paired enclosure and control plots, often with a blocked design in which pairs were replicated in different locations. In some studies the replicate blocks including paired



exclosure-control plots were located in somewhat different forest habitat types (e.g., [51]). We nevertheless considered these to be replicates encompassing variation in habitat types across the landscape of interest.

There were too few studies on lichens to conduct meta-analyses, but effects of herbivory on lichen abundance were always negative or not statistically significant (Additional file 7, Column AO).

Data synthesis

Quantitative data were extracted from 103 of the 144 studies included in this review. In the other 41 studies, findings were not meta-analysable because variability and/or sample sizes were not available or could not be extracted with sufficient accuracy from graphs or statistical tables, or because none of the reported outcomes were of a kind that we had prioritised (see "Methods").

Table 2 Distribution of included studies over different forest cover types

Forest cover type	Examples of dominant tree species	No. of studies
Temperate broadleaf/mixed	<i>Acer</i> spp., <i>Quercus</i> spp.	80
Boreal broadleaf/mixed	<i>Betula</i> spp., <i>Populus tremula/tremuloides</i>	15
Poor-soil forest	<i>Pinus</i> spp., <i>Betula pubescens</i> ssp. <i>czerepanovii</i>	19
Richer-soil conifers	<i>Abies</i> spp., <i>Tsuga</i> spp., <i>Picea</i> spp., <i>Taxus baccata</i> , <i>Thuja plicata</i> , <i>Pseudotsuga menziesii</i>	19
Open woodland	<i>Eucalyptus</i> spp. (Australia) or <i>Betula</i> spp., <i>Quercus</i> spp. (European wooded pastures or meadows)	11
Regenerating	<i>Pinus sylvestris</i> , <i>Populus tremuloides</i>	12

Some of the studies appear more than once in the table, since they reported on more than one cover type

Table 3 Quantitative data on grazing/browsing pressure (herbivore density and biomass)

Study type	Herbivore density (no. of animals/km ²)		No. of studies
	Range	Median	
All studies	0.7–130	20	84
Wild ungulates (any intervention)	0.7–130	15.5	73
Livestock (any intervention)	1.2–123	25	14
Fencing (exclusion/enclosure, any species)	0.7–125	16.3	77
Sustained/abandoned/resumed livestock grazing	25–50	45	3
Study type	Herbivore metabolic biomass (kg/km ²)		No. of studies
	Range	Median	
All studies	15–10300	500	84
Wild ungulates (any intervention)	15–10300	465	73
Livestock (any intervention)	114–5500	2000	14
Fencing (exclusion/enclosure, any species)	15–3600	480	77
Sustained/abandoned/resumed livestock grazing	2750–5500	5000	3

The table is based on study averages (presented as ranges and medians) of grazing/browsing pressure in areas exposed to high herbivory (e.g. unfenced control plots in fencing studies). Reported herbivore densities have been converted by us to metabolic biomass (see Additional file 6), and livestock densities have been adjusted for length of grazing season (see "Methods"). Note that quantitative data on grazing pressure were available for only three of the 17 studies of sustained/abandoned/resumed grazing by livestock (or reindeer) included in the review

The extracted results consist of a total of 1317 comparisons across time and/or space of plants or invertebrates exposed to different levels of ungulate herbivory. Most of the data refer to the cover (440 comparisons), stem density (316), biomass (55), height (76) or species richness (240) of plants, or to the abundance or species richness of invertebrates (54 and 25 comparisons, respectively). Although quite heterogeneous, this evidence base was large enough to allow us to perform a fairly extensive set of meta-analyses.

Overall effects of ungulate herbivory on vegetation

As expected, there was considerable scatter between comparable outcomes from different studies. For example, the abundance of a given vegetation group could show positive responses to ungulate herbivory in some studies and negative responses in other ones; however, most of the individual effect sizes were not statistically significant, having large confidence intervals that included zero (see Additional file 8).

Averaged across studies, herbivory effects on vegetation abundance varied in magnitude among the major plant groups but were always either negative or not statistically significant (Fig. 3). For the abundance of understorey vegetation as a whole we found a negative response to herbivory. This was also the case for woody understorey as a whole, tree saplings (height > 1.5 m, dbh < 5 cm), shrubs, and bryophytes. In contrast, the abundance of saplings of unspecified size (or sizes that agreed only partially with our definition of saplings), tree seedlings (large and small), graminoids, and forbs showed no significant response.

A comparison between the two main metrics of abundance (cover and stem density) revealed that understorey vegetation as a whole responded negatively to herbivory when measured as cover (SMD: -0.77 , CI -1.14 , -0.39 , $n=52$) but not when measured as stem density (SMD: -0.03 , CI -0.35 , 0.29 ; $n=7$).

Among individual tree genera, abundances of *Quercus* and *Tsuga* saplings/seedlings responded negatively to

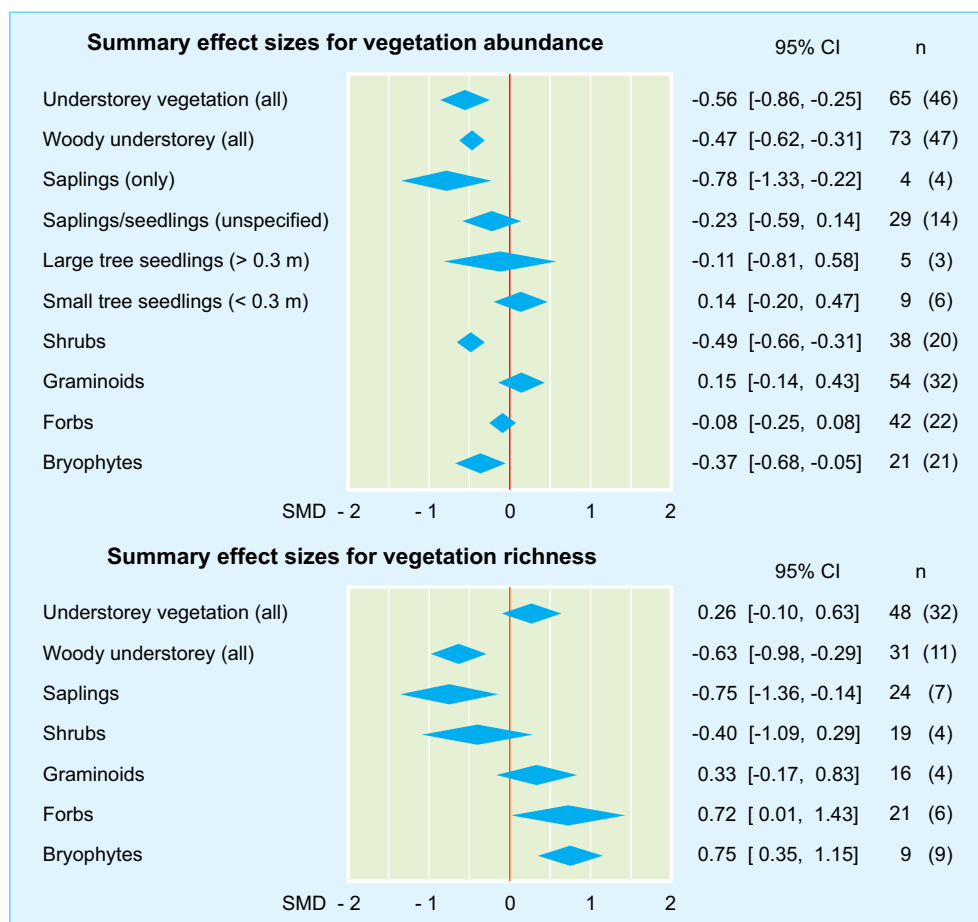


Fig. 3 Responses of vegetation abundance and species richness to ungulate herbivory. The diamond-shaped symbols show summary effect sizes (standardised mean differences), with 95% confidence intervals indicated by the widths of the symbols. A positive summary effect size indicates that the abundance or richness was higher at high herbivory than at low herbivory, and vice versa. Sample sizes (n) refer to the number of comparisons on which summary effect sizes were based, with the number of independent sites (or sets of sites) given in brackets

herbivory, whereas we found no statistically significant response in *Abies*, *Betula*, *Corylus*, *Fagus*, *Fraxinus*, *Pinus*, *Populus*, *Sorbus*, *Tilia* and *Ulmus* (Fig. 4). There were negative impacts of herbivory on sapling/seedling height for *Acer*, *Betula* and *Fraxinus* but not for *Populus* and *Quercus* (Fig. 4). These findings are primarily based on data on saplings (height > 1.5 m, dbh < 5 cm); however, we also included data from studies that reported on saplings of unspecified size or sizes that agreed only partially with our definition of saplings, or only on seedlings within the 0.3–1.5 m height range.

Among the individual plant species that we had selected for analysis, we found a positive response to herbivory in the abundance of *Alliaria petiolata*, which is regarded as invasive in North America. There were negative effects of herbivory on abundances of *Calluna vulgaris*, *Maianthemum canadense* and *Vaccinium vitis-idaea*, whereas *Deschampsia flexuosa*, *Empetrum*

nigrum, *Microstegium vimineum* (also invasive in North America), *Trillium* spp. and *Vaccinium myrtillus* showed no significant response (Fig. 4).

There was no statistically significant effect of ungulate herbivory on the species richness of understorey vegetation as a whole (Fig. 3). Among the subgroups of vegetation, we found a positive effect on species richness in forbs and bryophytes but a negative response in saplings and in woody understorey as a whole. The species richness of shrubs and graminoids showed no significant response.

Across studies, changes in understorey species richness were related to changes in understorey abundance (Fig. 5). This relationship was mostly due to reductions of species richness occurring only where the abundance of understorey vegetation was also reduced.

Two studies provided comparable data on native and exotic understorey vegetation. According to them, the

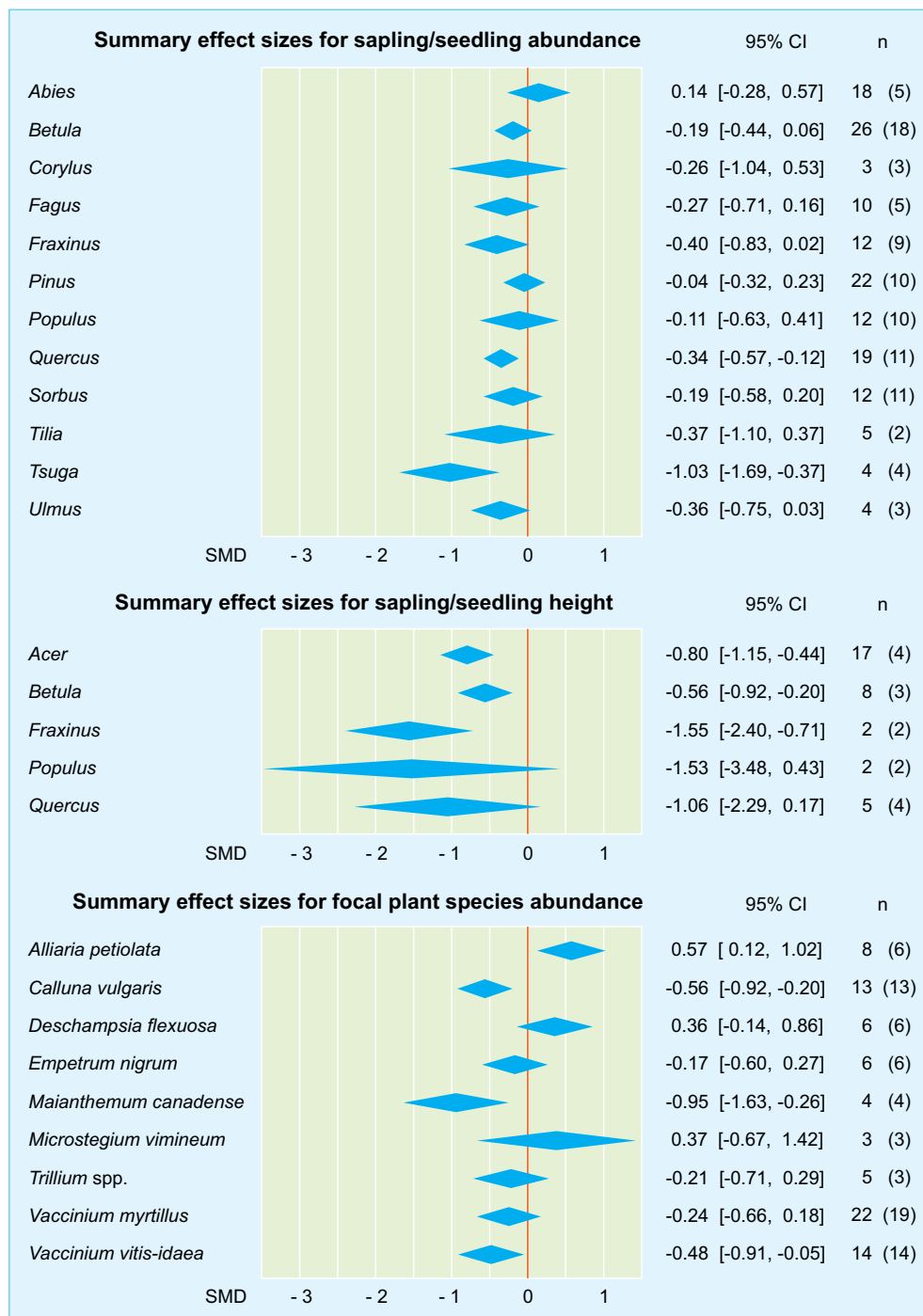


Fig. 4 Responses of sapling/seedling abundance, sapling/seedling height and focal plant species abundance to ungulate herbivory. See Fig. 3 for explanations

richness of exotic plants tended to respond more positively to herbivory than that of native plants (SMD: 0.71, CI 0.15, 1.27, n = 15, and SMD: -0.05, CI -0.56, 0.47, n = 15, respectively), but the difference was not statistically significant (Additional file 8).

Data on the survival of tree seedlings and on flowering and other measures of sexual reproduction in plants were too limited and heterogeneous to permit specific conclusions. Nonetheless, taken collectively across all

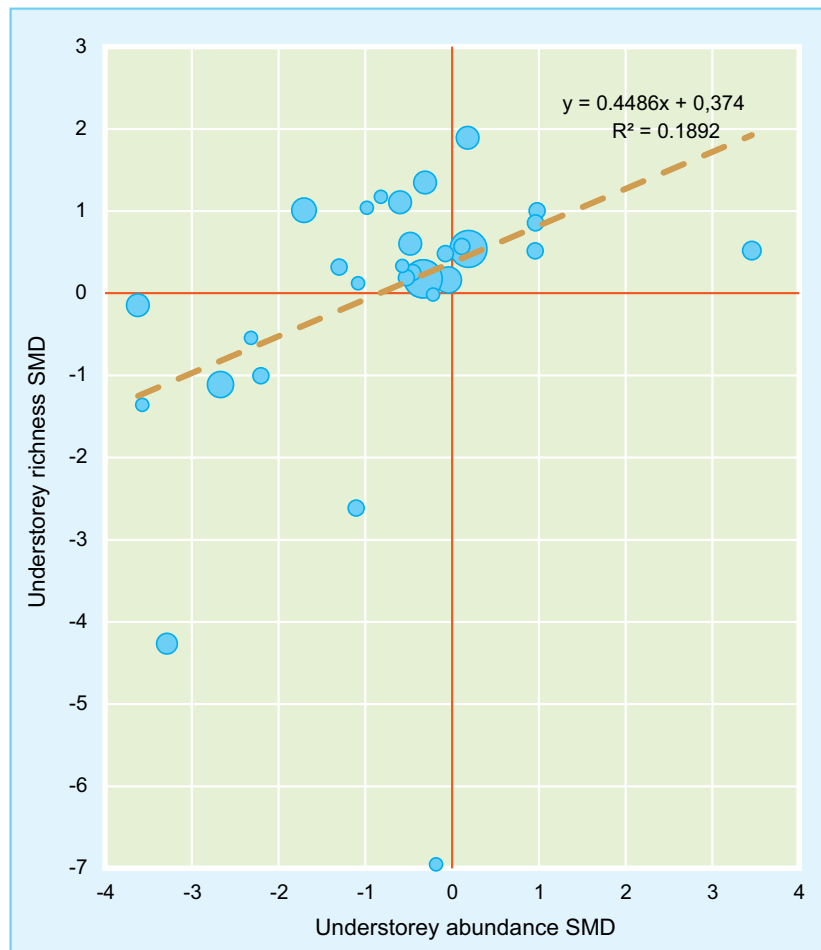


Fig. 5 Response of understorey richness vs. response of understorey abundance to ungulate herbivory. Each symbol represents a set of study plots from which data were reported on both richness and abundance. For calculation of the regression, data were weighted based on sample size (as indicated by the sizes of symbols). The outlier at the bottom is one of several data points from Pekin et al. [52] (low vs. zero cattle density at unburned sites; $n = 2$). If it is excluded, R^2 increases to 0.32

species, the data on plant reproduction showed a negative response to herbivory (Additional file 8).

Modifiers of herbivory effects on plants: subgroup analyses

The effects of herbivory on the abundance and richness of understorey vegetation as a whole depended on the origin of the ungulate (Fig. 6). The response was negative for abundance 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 responded positively to grazing by domestic ungulates, but there was no statistically significant effect of native or introduced wild ungulates.

The abundance of woody understorey vegetation responded negatively to all categories of ungulates (except the mixed one), and there were negative effects

of herbivory by native or introduced wild, but not domestic, ungulates on the species richness of woody understorey. Graminoid abundance showed a negative response to domestic ungulates but not to wild species (native or introduced), and graminoid richness was not affected by domestic grazers. Forb abundance responded to none of the types of herbivores, but there was a positive response of forb richness to grazing by domestic ungulates.

We found similar differences when we compared effects of ungulates with different feeding strategies (Fig. 7). There was a negative response of understorey abundance to 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 responded

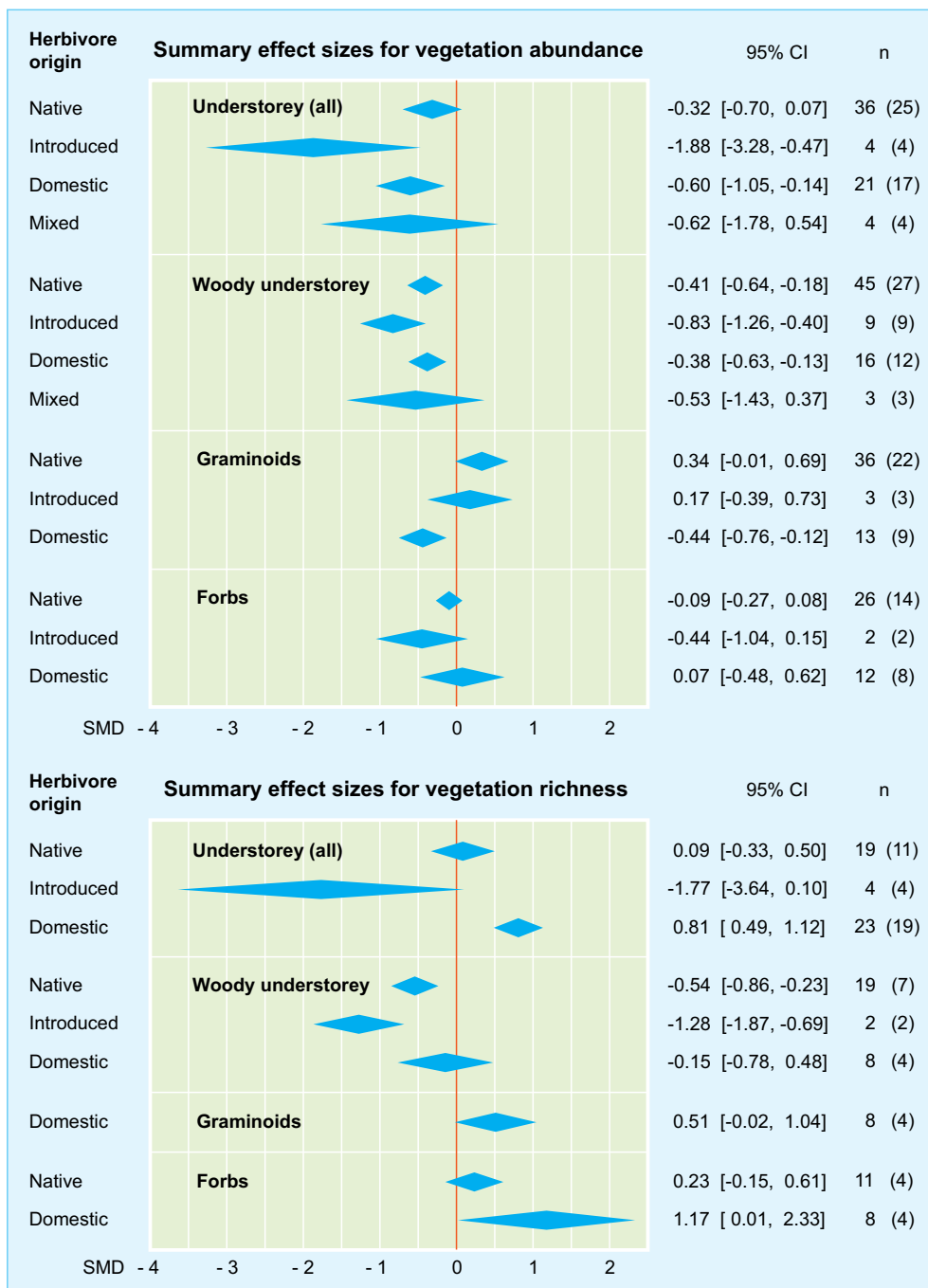


Fig. 6 Responses of vegetation abundance and richness to herbivory by ungulates of different origin. See Fig. 3 for explanations

positively to grazers but not to browsers or intermediate grazers/browsers.

We also found clear differences between effects of certain kinds of intervention (Fig. 8). In particular, while there were positive effects of herbivory on understorey species richness in the observational studies of sustained/

abandoned/resumed livestock grazing, such effects were generally absent where ungulates (wild or domestic) had been excluded or kept at reduced densities 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

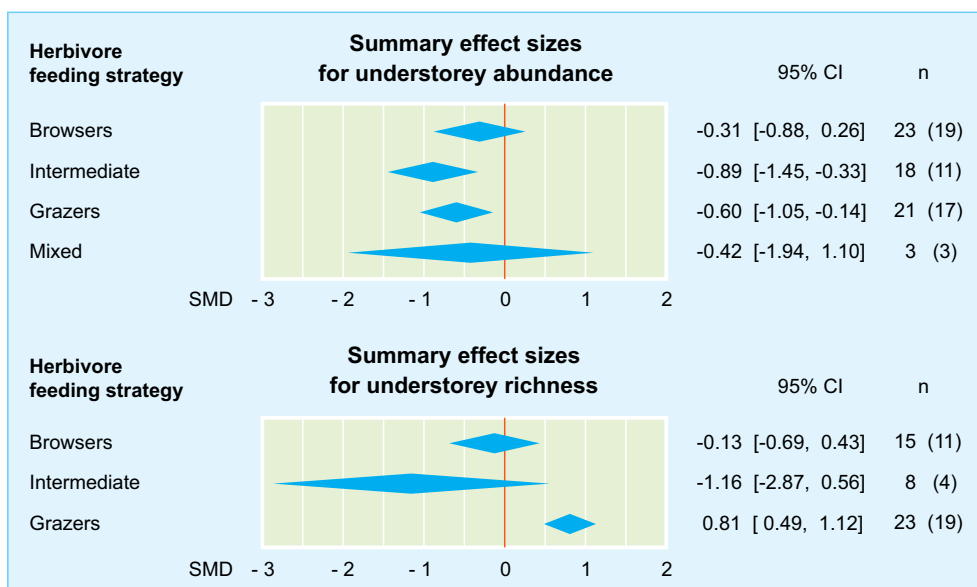


Fig. 7 Responses of understory abundance and richness to herbivory by ungulates with different feeding strategies. See Fig. 3 for explanations. Note that the ‘grazer’ category in this figure is identical to the ‘domestic’ category in Fig. 6

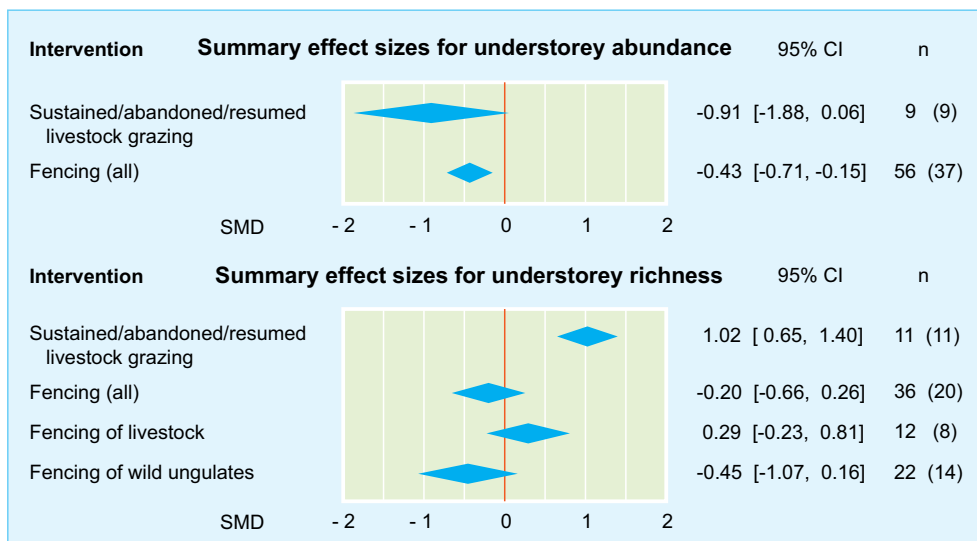


Fig. 8 Responses of understory abundance and richness to different kinds of herbivory manipulation. See Fig. 3 for explanations. As in other figures, a positive summary effect size indicates that the abundance or richness was higher at high herbivory than at low herbivory, and vice versa

studies of wild ungulates, but this difference was not statistically significant. Interestingly, fencing studies showed a negative impact on understory vegetation abundance, but the (far fewer) studies of sustained/abandoned/resumed grazing showed no such effect.

Studies of the effects of culling and of enhanced herbivory (achieved by means of enclosures and/or supplementary feeding) were too few to be meta-analysed

separately. Exclusion of these studies made no difference to the statistical significance (or non-significance) of abundance or richness responses to herbivory of any major group of vegetation (tested but not shown).

When separating study areas by forest cover types (Fig. 9), we found that the response of understory abundance to herbivory was negative only in temperate broad-leaf/mixed forest and in stands dominated by ‘richer-soil

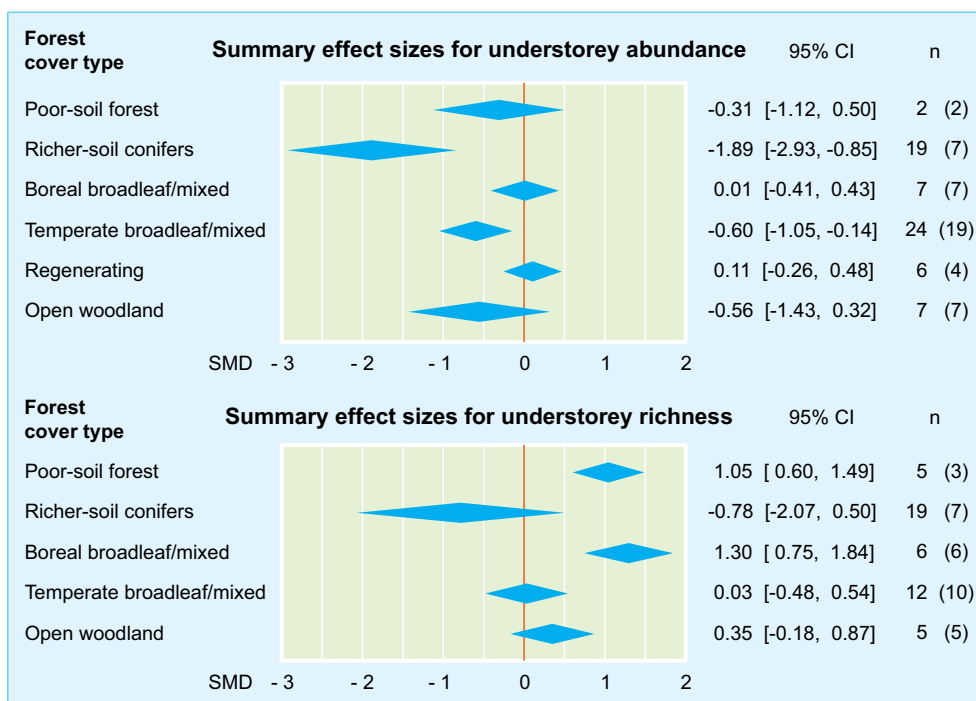


Fig. 9 Responses of understory abundance and richness to herbivory in sites with different forest cover types. See Fig. 3 for explanations

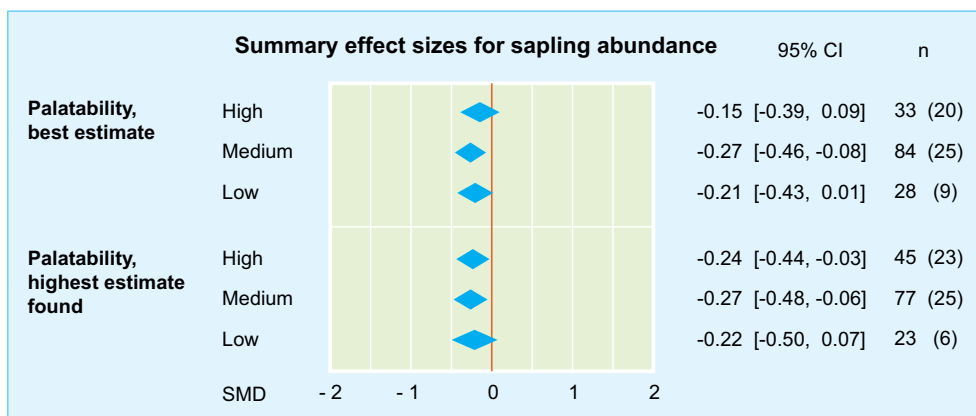


Fig. 10 Responses to ungulate herbivory of the abundance of sapling species with different palatability. Two different sets of palatability estimates were used. See Fig. 3 and Additional file 5 for explanations

conifers’ (conifers other than *Pinus*). In contrast, we found a positive response of understory richness in boreal broadleaf/mixed forest and in stands that we categorised as ‘poor-soil forest’ (usually dominated by *Pinus*). It should be noted that about half of the studies with data from richer-soil conifer stands had been performed in areas where dominant ungulates had been introduced or re-introduced into the wild. Studies of poor-soil sites had largely been conducted where the dominant ungulates

were intermediate grazers/browsers (e.g. *Cervus* or *Rangifer*) or grazers (livestock) rather than browsers such as *Odocoileus*.

The abundances of saplings of tree species with high, medium and low palatability all showed similar negative responses to herbivory (Fig. 10). With our ‘best estimates’ of palatability, the response was statistically significant only for species with medium palatability, whereas analyses based on the highest palatability estimates that we



had recorded showed significant responses for species with both high and medium palatability.

Effects of herbivory on the species composition of understorey vegetation had been reported by 26 studies. In cases where ordination diagrams and/or statistical tests indicated clear composition differences between areas exposed to high versus low (or no) herbivory, ungulate herbivory had been manipulated for an average of 18 years. Where no such differences were seen, the duration of manipulation had been shorter (7 years on average). No other statistically significant differences of effect modifiers were found between studies with and without indications of compositional differences.

Modifiers of herbivory effects on plants: meta-regressions

Weighted meta-regression of effect sizes against the duration of herbivory manipulation revealed that the abundance of forbs increased with increasing duration, and that the species richness of saplings and of woody understorey as a whole decreased (Fig. 11; Additional

file 9). No statistically significant impacts were detected on the abundance or species richness of other major sub-groups of vegetation or of understorey vegetation as a whole.

Intervention strength expressed as the difference in herbivore density or herbivore biomass between areas with high and low herbivory had relatively small impact on the abundance and species richness of vegetation. The only statistically significant effects were a reduction of the total understorey abundance with increasing herbivore density and a reduction of the abundance of woody understorey with increasing herbivore density and biomass (Fig. 11). Similar analyses that only included studies of the most commonly investigated ungulate genus, *Odocoileus*, revealed no significant response to increasing animal density within the range studied (not shown).

Somewhat clearer effects appeared in meta-regressions against intervention strength based on herbivore years (Fig. 11). With an increase of the number of herbivore years, we found (1) decreasing abundance of understorey

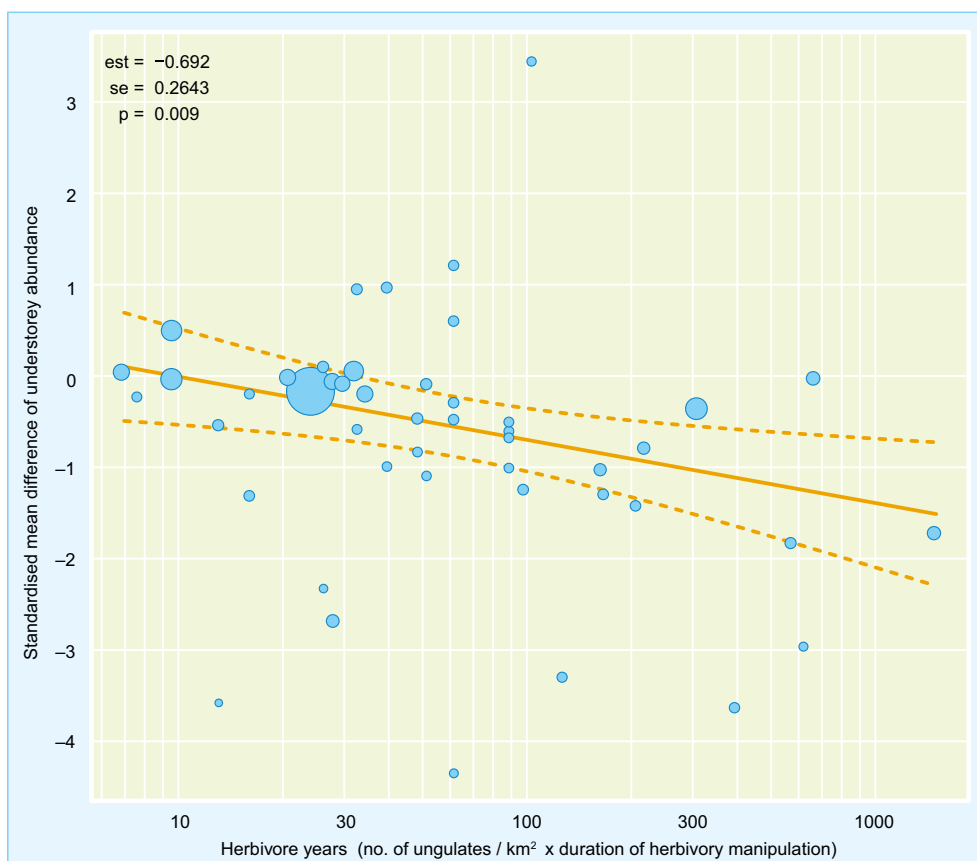


Fig. 12 Meta-regression of herbivory impacts on understory abundance vs. intervention strength based on herbivore years. Symbol sizes indicate statistical weights based on inverse variance

as a whole (Fig. 12), of woody understory 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 in meta-regressions against intervention strength based on herbivore biomass years (Fig. 11). The only statistically significant impacts found in the latter analyses were a decrease of the abundance of woody understory and an increase ($p = 0.050$) of the abundance of forbs.

With increasing mean annual temperature, ungulate herbivory had increasingly negative effects on the species richness of understory as a whole, woody understory and saplings (Fig. 13). Similarly, with increasing mean annual precipitation, herbivory had increasingly negative effects on the abundance of shrubs and on the species richness of saplings and understory as a whole.

The negative influence of temperature on the response to herbivory of understory richness was reflected by an even stronger positive influence of latitude (distance from the equator, Fig. 13). Both of these relationships

were partly due to the positive response of understory richness commonly reported in studies of sustained/abandoned/resumed livestock grazing, most of which were performed in cool, high-latitude parts of Europe (e.g. [12, 53–55]). The influence of temperature remained statistically significant when livestock studies of this kind were excluded from the analyses, but the influence of latitude did not. More positive effects at higher latitudes were also found in the abundance and richness of forbs, but only the abundance relationship remained significant when studies of sustained/abandoned/resumed livestock grazing were excluded (not shown).

Analyses of the correlations between different effect modifiers (Additional file 10) showed the expected strong co-variation between the four measures of intervention strength (r ranging from 0.51 to 0.89), between duration of manipulation and intervention strength based on herbivore years or herbivore biomass years ($r = 0.59$ and 0.69 , respectively), and between latitude and temperature ($r = -0.66$). Some co-variation, likely reflecting the



relatively high proportion of livestock studies in northern Europe, was also found between latitude and duration of manipulation ($r=0.31$) and between latitude and intervention strength based on herbivore biomass ($r=0.23$) or herbivore biomass years ($r=0.31$).

Effects of ungulate herbivory on invertebrates

The limited amount of data on invertebrates in studies included in this review restricted our ability to analyse effects of ungulate herbivory on these taxa. The abundances of lepidopterans and spiders showed negative responses to herbivory, but their species richness did not respond significantly (Fig. 14). For carabids there was a tendency for positive effects of herbivory on abundance and richness, but these effects were not statistically significant.

Impacts of study design, statistical treatment and publication bias

To assess the robustness of our analyses, we tested the impact of study validity on some of our findings. The mean response of understorey abundance to herbivory was of similar magnitude in high- and medium-validity studies. However, while the response was negative in the high-validity studies (SMD: -0.45 , CI $-0.69, -0.21$, $n=47$), it was not statistically significant in the medium-validity ones (SMD: -0.57 , CI $-1.22, 0.08$, $n=18$), since the outcomes of the latter were more divergent. The mean response of understorey species richness was close to zero in high-validity studies (SMD: 0.09 , CI $-0.31, 0.49$, $n=31$), whereas it tended to be positive (but not significantly so) in medium-validity studies (SMD: 0.48 , CI $-0.07, 1.03$, $n=17$). This means that conclusions

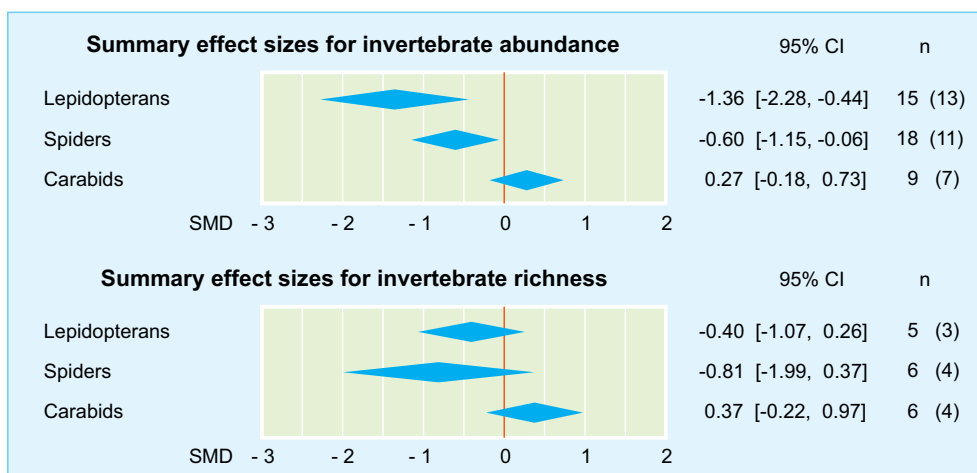


Fig. 14 Responses of invertebrate abundance and species richness to ungulate herbivory. See Fig. 3 for explanations

on understorey responses based on all available studies (negative impact on abundance, no change of richness, cf. Fig. 3) remained unchanged when only high-validity studies were included.

In studies based on fencing to exclude or enclose ungulates, understorey abundance generally responded negatively to herbivory (Fig. 8). However, while this result was statistically significant where exclosures/enclosures were larger than 0.1 ha (SMD: -0.52, CI -0.81, -0.23, n=32), it was not significant where they were smaller (SMD: -0.41, CI -0.87, 0.05, n=24).

Pseudoreplication was involved in two of 65 extracted comparisons of understorey abundance and in two of 48 comparisons of understorey richness. When pseudoreplicated data were excluded, summary effect sizes changed only slightly (from SMD: -0.56, CI -0.86, -0.25, n=65 to SMD: -0.48, CI -0.75, -0.21, n=63 for abundance and from SMD: 0.26, CI -0.10, 0.63, n=48 to SMD: 0.28, CI -0.10, 0.67, n=46 for richness).

For four of the 65 comparisons of understorey abundance and four of the 48 comparisons of understorey richness, study authors had not provided overall means and variability. In such cases we calculated effect sizes based on individual data for replicated plot pairs instead. Summary effect sizes changed only slightly (to SMD: -0.57, CI -0.88, -0.26, n=61 for abundance and to SMD: 0.26, CI -0.12, 0.64, n=44 for richness) when these calculations were made with the alternative method (described above) as compared to the one we normally used.

When mapped in a funnel plot, understorey abundance data show a slight asymmetry suggesting the possibility of publication bias (Fig. 15)—it indicates that studies with high precision (due to a large number of observations) generally reported effect sizes somewhat closer to zero

than studies with lower precision. It is less clear whether such an asymmetry is also present in the funnel plot for understorey richness, even if it does contain a few outliers (Fig. 15).

Discussion

Our review revealed a large body of high-validity experimental studies on biodiversity impacts of ungulate herbivory in forests. We acknowledge that this does not represent the whole knowledge base on the subject: for instance, we excluded unreplicated studies of the kind that predominated before the ‘experimental era’ (many of which were summarised by Adams [4]). However, the systematic review method enabled us to identify a relevant selection of studies with a minimum of bias and subjectivity. We have meta-analysed the impacts of grazing and browsing on vegetation and invertebrates, exploring multiple potential conservation targets.

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.

The overall effects documented by our meta-analyses included the following:

1. Ungulate herbivory generally reduced understorey vegetation abundance, although certain plant groups—tree seedlings and herbaceous vegetation (forbs and graminoids)—showed no significant response (Fig. 3). Our analyses thus do not support the generality of some patterns identified in earlier conventional reviews, such as an increase in bryophyte cover due to competitive release from forbs

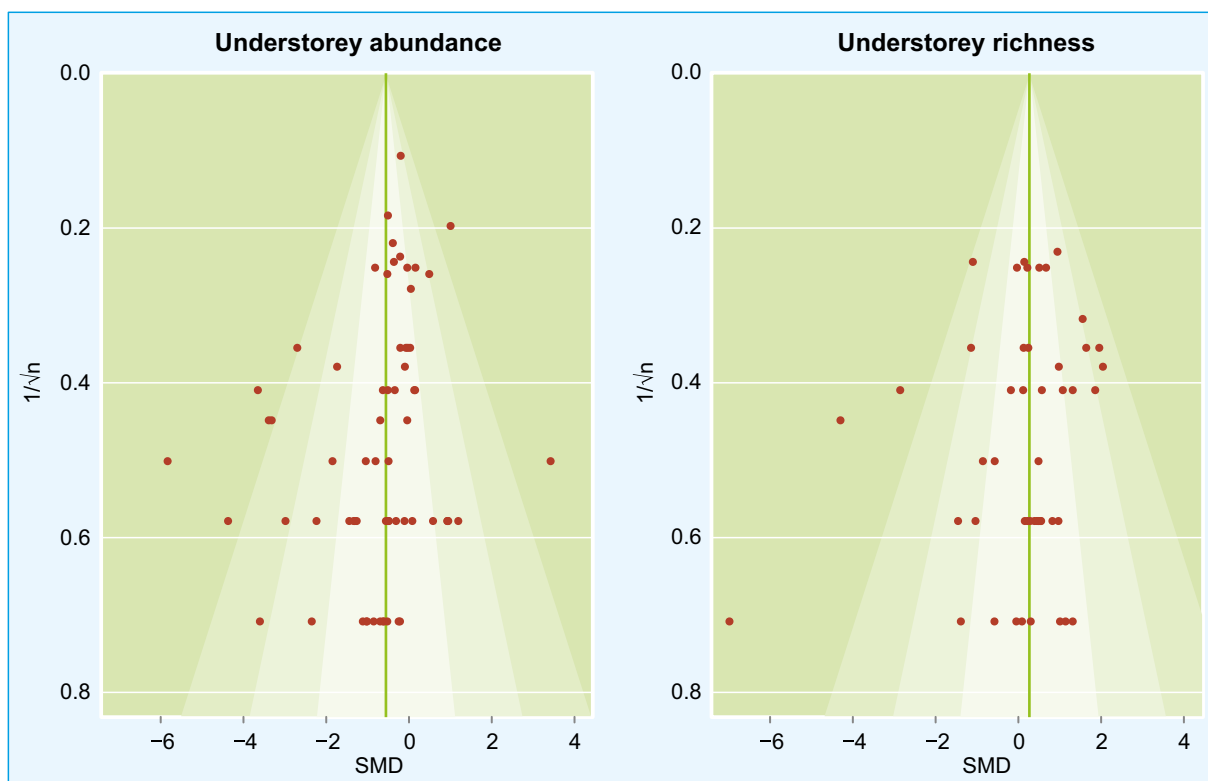


Fig. 15 Funnel plots for responses of understorey abundance and richness to ungulate herbivory. The inverse square root of the sample size is used as a measure of precision. Background shadings have been applied to facilitate comparison but have no particular significance

[8] or an increase of grasses [11]. A positive impact of herbivory on tree seedling establishment [8, 40] was also not confirmed; however, the non-significant effect on small seedlings differed distinctly from the clear negative effect on saplings (Fig. 3; see also [6]).

2. At the scale of study plots (which in most cases ranged between 100 m² and 10 ha), manipulation of herbivory produced no change of the species richness of understorey vegetation as a whole (Fig. 3). Among plant groups, only woody vegetation became less species-rich when grazed or browsed, an effect that has been supported by previous meta-analyses restricted to deer impacts [7, 10]. In contrast, species richness of forbs and bryophytes increased, despite the latter experiencing abundance reduction. In brief, the vegetation reduction caused by ungulate herbivory produced variable changes in plant species richness, probably because of multiple interacting direct (increased light to the herbaceous or ground layer; trampling disturbance) and indirect impacts (shifts in competitive and protective relationships within vegetation). However, our sample of studies did not include a single case where

total understorey species richness declined without a concomitant reduction in understorey vegetation abundance (Fig. 5).

3. The negative effect of ungulate herbivory on tree regeneration—a major motivation for controlling grazing/browsing pressure in forests—was not uniformly spread among tree taxa. Negative effects on sapling/seedling abundance were only confirmed for *Quercus* sp. and *Tsuga* sp. (Fig. 4). This result cannot simply be attributed to low power due to scarcity of studies, because several other genera (e.g. *Abies*, *Pinus*, *Populus*, *Betula*, *Fraxinus*) were covered by a relatively large number of studies. Yet, as exemplified by *Acer*, *Betula* and *Fraxinus*, herbivory can still reduce the average sapling/seedling height. Our review did not specifically address the extreme scenario where arrested height growth results in complete lack of recruitment to the tree layer despite abundant regeneration (e.g., [56]).

4. Analyses of individual native understorey species showed negative summary effect sizes for all dwarfshrubs tested, although the effects were significant only for *Calluna vulgaris* and *Vaccinium vitis-idaea* (Fig. 4). Ungulate herbivory also had a negative

impact on the forest-dependent, shade-tolerant forb *Maianthemum canadense* and a similar (but non-significant) effect on *Trillium* spp.

5. The two analysed understorey plant species that are categorised as invasive (in North America) both showed positive responses to herbivory, significantly so for *Alliaria petiolata* but not for *Microstegium vimineum* (Fig. 4). Although only two studies provided comparable data on native and exotic vegetation, they showed a positive effect of herbivory on the richness of exotic plants but not of native ones.
6. Ungulate herbivory had negative effects on the abundance of lepidopterans and spiders but not carabids (Fig. 14). These results could be explained by the reliance of lepidopterans and many spiders on understorey vegetation, the abundance of which was reduced by herbivory [16]. A herbivory-caused reduction of spider abundance has also been demonstrated in a meta-analysis focused primarily on grasslands [57]. Complex canopies and a dense understorey provide important shelter for spiders in winter and a third dimension for spinning nets [58]. However, contrasting with previous reviews [16] and meta-analyses [14], we found no significant effects on the richness of any of these three groups of invertebrates in forests.

Reasons for heterogeneity

A major finding of our review was that the context (regional climate, forest type, management history and herbivore identity) profoundly affects the impacts of ungulate herbivory on biodiversity, and this has practical implications for forest conservation. A similar conclusion was previously reached by a systematic review on the impacts of reindeer/caribou on arctic and alpine vegetation [59].

Specifically, we identified the origin of herbivores as important for determining their influence on understorey vegetation abundance and richness. While livestock and introduced wild ungulates had negative impacts on the abundance of understorey as a whole, native wild ungulates or mixtures of native and introduced wild ungulates had no significant effects (Fig. 6). Livestock, representing true grazers, were also the only herbivores that negatively impacted graminoid abundance, increased total understorey species richness (see also Fig. 7), and did not reduce the species richness of woody understorey vegetation. One possible explanation is that true grazing regulates competition and opens up space within the field layer more effectively than browsing. Together these results suggest that forest vegetation is more sensitive to novel herbivory regimes associated with introduced deer or livestock than to native herbivores; this is probably

because of a lack of historical adaptation combined with (often) high grazing/browsing pressure associated with introduced or domestic herbivores. Co-evolutionary history with mammalian herbivores has also been hypothesised to explain geographically distinct responses of beetles to herbivory [60], but case studies on invertebrates are still too scarce for a meta-analysis of effect modifiers.

The differences between intervention types also exhibited some interesting patterns. Fencing studies, which were by far the most common, showed no effect of herbivory on understorey species richness (Fig. 8). In contrast, studies of sustained/abandoned/resumed livestock grazing showed a positive effect on understorey richness, despite much smaller sample size. One conceivable explanation is that studies of the latter type tended to report on effects over a longer time period, which might better capture slow changes in plant assemblages. However, while our comparison of studies with stable vs. changed species composition supported such an influence of the duration of herbivory manipulation, plant subgroup responses did not fully support it. Effects of herbivory on forb abundance became increasingly positive with duration, while effects on woody plant richness (and separately on sapling richness) became increasingly negative (Fig. 11). The latter result has also been reported in a previous meta-analysis on white-tailed deer impacts, where it was explained as a consequence of rapid recruitment of local tree species [10]. Thus, the positive species richness response to herbivory in the case of sustained/abandoned/resumed grazing may include a combination of the effects of herbivore type (livestock only) and duration.

Forest cover type was an important factor modifying the responses of understorey abundance and richness to ungulate herbivory, which reflects the resilience of different ecosystems to grazing/browsing pressure. The negative effects on understorey vegetation abundance were significant only for the richer-soil conifer and temperate broadleaf/mixed forest types (Fig. 9). The fact that ungulates did not affect species richness in these forest ecosystems suggests that other plant species have limited capacity to become established there when herbivory opens up space in the understorey. The main effect on understorey vegetation in such forests may thus be an impoverishment at high herbivore densities; thus when grazing/browsing pressure is removed these systems might have a relatively good potential to recover [19]. In contrast, while the overall analysis showed no significant effects of herbivory on understorey richness, the subgroup analysis uncovered positive effects in the poor-soil and boreal broadleaf/mixed forest types; these effects were not accompanied by understorey abundance

change. Hence, these forest types might be particularly responsive to disturbance by herbivory in terms of new species being able to establish. On poor soils, some species may be favoured by the fertilising effect of ungulate dung (e.g., [61]).

It has been common knowledge that ungulates have a selective influence on forest stand composition due to the varying palatability of tree species (e.g., [6, 19]). It was thus surprising that we did not find any significant differences between mean responses to herbivory of the abundance of tree saplings with different palatability (Fig. 10). It is possible that the palatability effects were confounded by differences between herbivore species, herbivore densities or forest cover types.

Another common belief is that impacts of ungulates depend on their abundance, and some recent syntheses focused on finding threshold densities of animals for predicting or preventing ‘damage’ to the forest [13, 62]. However, while the negative impacts of herbivory on total understorey and woody understorey abundance did scale with the density of herbivores (regardless of herbivore species), our efforts to measure grazing/browsing pressure more accurately—for example by using herbivore biomass or biomass years instead—did not make our results much clearer (Fig. 11). On the other hand, while the abundances of forbs and graminoids showed no significant effects of high versus low herbivory, meta-regressions revealed that the effects of herbivory became increasingly positive with intervention strength based on herbivore years and herbivore biomass years, respectively. Effects on the richness of saplings became increasingly negative while effects on the richness of forbs became increasingly positive with intervention strength based on herbivore years, but there were no other scaling effects of the intervention strength on species richness. The release of above- and below-ground resources to the herbaceous layer that would accompany a reduction of woody vegetation possibly explains the positive relationship between grazing/browsing pressure and abundance of graminoids and forbs as well as forb richness.

Finally, several responses to herbivory varied with macroclimate: (1) the effects on total understorey richness and richness of saplings and woody vegetation as a whole became increasingly negative with increasing mean annual temperature, and (2) effects on shrub abundance, total understorey richness and sapling richness became increasingly negative with increasing mean annual precipitation (Fig. 13). These results were mirrored by the broad-scale pattern that herbivory impacts on forb abundance, total understorey richness, and forb richness trended towards being more positive at higher latitudes. Overall this evidence suggests that forests in warmer and wetter locations are more susceptible to species losses

due to herbivory; in turn, they might be able to respond more strongly to reductions in grazing/browsing pressure. However, the results might also be influenced by the many studies of sustained/abandoned/resumed livestock grazing in cooler, higher-latitude regions of Europe; these studies showed clear positive effects of grazing on understorey richness.

Review limitations

Our searches for literature in publication databases were all focused on forests with tree species commonly occurring in Sweden, which means that they did not provide a complete coverage of relevant studies made in the temperate and boreal climate zones. To compensate for that, we made considerable efforts to find additional literature in bibliographies of existing reviews of ungulate herbivory in forests, but we may still have missed a number of studies that fulfilled our criteria for inclusion. Nevertheless, we found satisfactory experimental evidence on herbivory impacts from temperate North America and Europe, boreal Fennoscandia and, for non-native ungulates, from New Zealand. These are regions where excess or absence of grazing and browsing have been identified as problems (e.g., [25, 26, 63]), both in protected areas and in production forests and agroforestry systems [29].

The scarcity of studies in boreal regions outside Fennoscandia (none found in Asia and European parts of Russia, few in North America) likely reflects the fact that ungulate herbivory has not been identified as a serious conservation issue in these regions, and there seems to be a paucity of scientists and little tradition of manipulative experiments, particularly in continental Asia [64]. However, there is no doubt that ungulate herbivory plays a role in these forests as well. The lack of research in cold continental climatic regions may hide some functionally distinct responses of biodiversity to herbivory, given that we found climate and forest type to strongly affect such responses.

Another major limitation of the evidence base was the scarcity of primary research on how ungulate herbivory affects invertebrates; this was particularly notable in comparison with the abundance of studies on vegetation and is troubling considering the huge diversity and ecological importance of invertebrates in forests. Due to this limitation, we were only able to analyse the overall responses of abundance and species richness in lepidopteran, carabids and spiders, which mostly represent aerial herbivores, ground-dwelling and vegetation-dwelling predators, respectively. We found almost no data on canopy-dwellers and parasitic species, and there were only a handful of studies on soil biota.

Our review also indicated that only limited research on ungulate herbivory has so far taken place in actual

protected areas. This may have prevented the detection of problems and responses that are especially relevant to (small) set-asides, which experience extensive external impacts and in which biotic assemblages are possibly depauperate compared to those in larger, pristine areas. For example, there appears to be very little research on how the lack of top predators (e.g., wolves, wolverines) affects herbivore pressure, or on how herbivory should be managed to address issues arising from modified regimes of wildfire and other natural disturbances. One reason for the lack of research in protected areas is that properly replicated inclusion/exclusion experiments may be difficult to reconcile with conservation regulations and with limitations of the space available for experimentation in small set-asides.

Studies of poor-soil stands (primarily pine forests) were relatively scarce. In Fennoscandia young pine forests are browsed by moose, and their response to herbivory manipulation is therefore of interest to managers (e.g., [65]). Also, we found few studies of herbivory effects on sparsely wooded habitats such as wooded grasslands, although these are clearly a conservation priority in Europe [39].

Quite a few experimental studies relevant to the topic of this review date back at least to the early twentieth century (e.g., [66, 67]). Some of them have provided an outstandingly long-term look at herbivory impacts (e.g., [68, 69]), but most of these studies were unreplicated. True replication is difficult to achieve in field-based studies of herbivory manipulation, but it is nevertheless critical for the scientific validity of the results, and we therefore excluded unreplicated studies from our review. In practice, our requirement of replication restricted the temporal scale of most herbivory effects reported by us to <20 years. This is a particularly important limitation in the context of tree-regeneration management in protected areas, where the 'escape' of a cohort of seedlings every 30 or 40 years may be sufficient to maintain a mixed age stand structure [26].

We also excluded a few studies where herbivory effects were confounded, e.g. due to grazed and ungrazed plots being subjected to different treatments in addition to the manipulation of ungulates. While combined treatments might often be applied in a management regime, we were not able to use studies if the herbivory effects could not be isolated.

We found that many studies suffered from a paucity of background information on, for example, forest type, age, basal area, density, and stand origin. More complete information on these characteristics would have allowed us to provide more insight into important effect modifiers. For example, the effects of opening up lower canopies by herbivores are probably influenced by the upper

canopy cover, and local species pools may differ depending on stand history.

Conclusions

Implications for policy/management

The main motivation for this systematic review was a lack of knowledge that managers could use to approach manipulation of ungulate herbivory to meet forest conservation objectives. Our review, with its quantitative meta-analysis approach based on many high-validity case studies, is thus a timely step towards clarifying the issue of ungulate herbivory for environmental managers.

The *woody understorey* vegetation component, which is often targeted by browsers, plays a critical role in stand dynamics. 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 (e.g., [70]). Our analysis identified some dominant tree genera for which reduction of ungulate herbivory could substantially benefit regeneration; these included, for example, *Tsuga* and *Quercus*, which were also previously regarded as vulnerable to ungulate herbivory [5, 71]. For other putatively browsing-sensitive genera (such as *Abies*, *Betula*, *Pinus* and *Populus*) our results suggest manipulation of herbivory pressure is less likely to be an effective management tool for regeneration. 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 (e.g., [72]); effects on sapling abundance are thus critical, as would be their survival and growth, which we unfortunately could not examine in detail.

Herbaceous understorey vegetation is of management interest for its conservation value and because it can influence tree regeneration. Our results demonstrate that ungulate herbivory does not generally pose a risk for eradication of plant species from this layer, although in certain sensitive assemblages or for certain ungulates this could be a concern. In the studies that we synthesised, light-demanding plants might have benefited from small-scale disturbances other than grazing that occurred in the low herbivory plots (e.g., [73]), but we were not able to control for this. Importantly, our results 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

(Fig. 8). Our review also confirmed that ungulate herbivory might benefit certain invasive plants.

Overall, our results 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.

Unfortunately, our results provide little clarity as to the forest types or regions in which manipulation of herbivory would be more or less effective. This can likely be attributed to the effects of confounding factors, a scarcity of studies in some forest types and regions, and the fact that effects are context-dependent [74], for example being a function of ungulate densities, the plant community, and its carrying capacity for herbivores.

We found that exact data on grazing/browsing pressure (as compared to the simple high/low herbivory contrast) was relatively uninformative in terms of predicting biodiversity responses. Further, we could not establish any general non-linear (threshold) responses to ungulate herbivory, although such responses have been found in some case studies and discussed as a basis for defining acceptable levels of ungulate abundance (e.g., [62]). Moreover, we found that understorey species richness was reduced only when understorey abundance was also reduced.

On the whole, our findings indicate that forests are relatively resilient to ungulate herbivory. This is perhaps not surprising given that ungulates have been a natural component of forest ecosystems for centuries or millennia [75]. Thus, there is limited evidence for *ungulate-caused ecosystem shifts* in forests; these are likely restricted to fewer cases than early warnings have indicated (e.g., [5, 17]).

To find symptoms of ungulate 'damage', therefore, managers should focus on specific evidence that the regeneration of a particular plant population or component of the vegetation might be endangered. It is known, for example, that a palatable plant species may become vulnerable when its local population is small (e.g., [47]), and that herbivory may 'arrest' succession in early phases of forest regeneration while speeding up later phases [76].

While the body of evidence that we present is useful as a documentation of effects of high herbivore pressure, it is less suitable for detecting those 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 optimise the positive impacts of grazing on herbaceous plant richness while at least occasionally releasing tree sapling cohorts [8]. The pervasive context-dependence demonstrated by our review further suggests that the balance between these two targets should be specified on a site-by-site basis using adaptive management approaches.

Implications for research

Our investigation of the primary literature on grazing and browsing impacts in forests revealed that the evidence base on the subject is large, but geographically uneven and ecologically heterogeneous.

The prevailing study approaches have at least two major limitations. First, since the mid-twentieth century, enclosure-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 [14, 16]). The majority of studies in our review compared plots inside and outside enclosures 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 studies that examine responses along a gradient of grazing/browsing intensity, including seasonal grazing and both upward and downward manipulation of herbivory (see also [8, 40]). The rare large-scale experiments that explored several levels of ungulate density (e.g., [77, 78]) have thus contributed unique insights into the complexity of biodiversity responses. There is a need for additional experiments of this kind. 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 (see also [79]), and we call for initiatives to analyse all currently available results that cover at least 20 years.

Certain improvements of the evidence base could be quite easy to achieve. When analysing data from studies included in the review, we frequently had to exclude potentially valuable findings because they lacked sufficient information about precision/variability and/or sample sizes. Similarly, even where estimates of precision

were provided, we were often frustrated by unclear or missing descriptions of how they had been calculated. In a number of cases we found reason to suspect that published standard errors were based on the variation among individual subsamples rather than the means of true replicates. In future studies, such shortcomings should be simple to avoid through more transparent reporting.

Given the high context-dependence of herbivory impacts, major knowledge gaps such as the lack of studies in boreal zones of Asia and North America should be filled by future research. Our review also revealed several gaps in the knowledge regarding herbivory effects on important groups of organisms. More research is required on the highly diverse invertebrate fauna, both on the ground, in the vegetation, and in the soil. Whenever possible, such research should establish causal links to observed changes in vegetation, since these are better understood and easier to measure in the field, and thus may constitute a useful indicator for managers. Data on bryophytes are also very scarce and do not even allow distinction between the impacts on major taxonomic (hepatics; mosses) or ecological subgroups (epigaeic, epiphytic and epilithic taxa). Even less information is available on lichens. Additionally, it would be important to understand ungulate impacts on the availability and quality of substrates for both bryophytes and lichens. Across all taxon groups, studies on species and populations of actual conservation concern are needed to complement assemblage-scale measurements, which are often too general to guide conservation efforts.

Similarly, there is surprisingly little research focused on the incidence of major ecosystem changes arising from changes or differences in ungulate herbivory. We call for documentation of ecosystem shifts to new relatively stable states under ungulate herbivory, and for analyses of the environmental conditions under which such shifts occur. Insights are also needed on how herbivory mediates impacts of pest outbreaks, invasive species, and abiotic disturbance regimes (such as accumulation of forest fuels or exposure of trees to wind).

Finally, we are happy to recognise a growing number of studies that examine more complex options for herbivory manipulation, although these studies do not yet allow for generalisation. The broadest issue, raised decades ago (e.g., [8]) but still with no satisfactory answer, is how to best combine active and passive management of ungulates for conservation purposes. Such approaches can include, for example, intermittent grazing or short-term reductions of ungulates to facilitate tree regeneration [80], flowering and seed production of herbs, or reproduction of vegetation-dwelling invertebrates. A more specific issue is how to combine ungulate manipulation with other options for conservation management,

such as thinning or prescribed burning. We also require a much better understanding of how impacts of herbivory interact with effects of natural disturbances and broad changes of land use. This will become more and more important because climate warming supports increases in ungulate densities in many temperate and boreal forests, while also increasing the probability of stand-replacing disturbances [81, 82]. The land-use processes that need to be studied are related to intensification of agriculture or silviculture around protected areas, or to abandonment of agriculturally marginal land. Such changes can affect protected areas through increasing the availability of forage for wild ungulates, altering the hunting pressure (which also affects animal movements), and influencing the occurrence of livestock grazing.

Additional files

- Additional file 1.** Literature searches (search update).
- Additional file 2.** Articles excluded as irrelevant to the review.
- Additional file 3.** Studies excluded due to low or unclear validity.
- Additional file 4.** Extracted data records.
- Additional file 5.** Assessments of palatability of tree species.
- Additional file 6.** Metabolic body mass of ungulate species.
- Additional file 7.** Narrative table (descriptions of all included studies).
- Additional file 8.** Forest plots.
- Additional file 9.** Meta-regressions.
- Additional file 10.** Correlations between potential effect modifiers.

Authors' contributions

The topic and design of this review were conceived by CB, BGJ, KJ, AL, EM, JM and JS. Searches for literature were made by CB and AL. Critical appraisal of studies was conducted by AL and EM, who also compiled the narrative synthesis. Extraction and meta-analyses of outcomes were performed by CB and BM. The manuscript was drafted by CB, AL and EM. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The dataset analysed in this review is available in Additional file 4.

Consent for publication

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