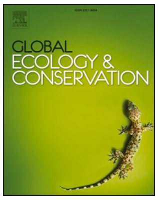
Global Ecology and Conservation 64 (2025) e03961

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Original research article

Context-dependent effects of deer on aboveground carbon stocks in the regenerative tree layer in temperate and boreal forests: A meta-analysis

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ARTICLE INFO

Dataset link: Context-dependent effects of deer on aboveground carbon stocks in the

ABSTRACT

Herbivores, including deer (Cervidae), influence ecosystem functions and carbon cycling by affecting vegetation structure and composition. Given the increase in deer populations in Europe and North America, there is growing interest in their impact on carbon dynamics in temperate

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https://doi.org/10.1016/j.gecco.2025.e03961
Received 6 May 2025; Received in revised form 10 November 2025; Accepted 11 November 2025
Available online 13 November 2025

regenerative tree layer in temperate and boreal forests: a meta-analysis

Keywords:
Deer
Herbivory
Carbon stocks
Forest
Wood density
Meta-analysis

and boreal forests. We investigated the effects of deer on carbon stored in the seedling and sapling layer through two mechanisms: (1) deer affecting the overall aboveground woody biomass in these strata and (2) deer changing the composition of tree species in these strata, because species differ in wood density and carbon content. We performed a meta-analysis of 17 datasets from 12 cases, assessing the effects of deer exclusion on aboveground carbon stocks within the seedling and sapling layer (≤ 3 m) under two scenarios of carbon calculation, where we used either: (1) species-specific carbon content and wood density values (mean scenario) and (2) generic carbon content and wood density values (neutral scenario). Most cases reported inconclusive effects of deer exclusion on aboveground carbon stocks, regardless of species-specific carbon content or wood density values. A total of 35 % of cases showed positive outcomes, indicating that an increase in carbon stocks within deer exclosures. Despite the short duration of cases, and high variation in effect sizes between them, we still found a small, significant difference between coniferous- and deciduous-dominated forest systems. The among-case variability in effects suggests a complex interaction between the impact of deer browsing and forest carbon. Understanding these interactions is vital to assess wildlife-carbon relations and to develop appropriate forest conservation approaches in response to growing deer populations.

1. Introduction

Global change and biodiversity loss have significantly affected ecosystems worldwide, with far-reaching impacts on ecosystem services (Rockström et al., 2009). These challenges are closely connected: biodiversity restoration has the potential to contribute to climate change mitigation (Cromsigt et al., 2018; IPBES, 2019; IPCC, 2019; Shin et al., 2022), and plant diversity and carbon storage are intimately linked—higher plant species richness has been linked to higher soil carbon (Lange et al., 2015; Steinbeiss et al., 2008), aboveground biomass (Poorter et al., 2015), and aboveground and belowground carbon stocks (Liu et al., 2018). In turn, plant diversity can be heavily influenced by animal activity, in particular herbivory, resulting in animal-mediated effects on ecosystem carbon. Wild ungulate herbivory can cause reductions in forest soil organic carbon (Marks et al., 2024), and wild ungulate exclusion can have a positive effect on the aboveground biomass of certain species (Ritchie et al., 1998) or species richness of species groups such as forbs and bryophytes (Bernes et al., 2018). High densities of wild deer have been found to increase soil nutrients via faecal waste and urine deposition, increase understory community heterogeneity, and even increase deciduous sapling densities (Jensen et al., 2011). Herbivory can also mitigate woody encroachment in the northern hemisphere (Olofsson et al., 2009), potentially preventing albedo-driven warming that outpaces carbon sequestration via increased woody biomass (de Wit et al., 2014). More generally, recent work suggests that wild animals can have potentially significant effects on the carbon cycle (Schmitz et al., 2014, 2018). These examples underlie the concept of "animating the carbon cycle": restoring wild animal populations and their ecological functions to contribute to ecosystem carbon capture (Cromsigt et al., 2018; Schmitz et al., 2018). However, the effectiveness of this approach depends on a deeper understanding of animal-carbon relations. Not all species affect carbon dynamics equally (Schmitz et al., 2023), and impacts vary with species traits and environmental context (Duvall et al., 2024; Malhi et al., 2022; Schmitz et al., 2023).

In the northern hemisphere, deer populations (family Cervidae) have increased in number and expanded their distributions (Burbaitė and Csányi, 2009, 2010; Côté et al., 2004; Linnell et al., 2020; Valente et al., 2020). These species can significantly alter their surrounding environment through their foraging, nutrient translocation, and trampling (Bardgett and Wardle, 2003). Deer herbivory can strongly alter forest vegetation structure by altering the height, density, and architecture of woody plants (Churski et al., 2024; Côté et al., 2014; Hidding et al., 2012; Kullberg and Bergström, 2001; López-Sánchez et al., 2021), leading to deer-mediated changes in aboveground woody biomass in the seedling and sapling layer from forest floor to understorey (Ammer, 1996; White, 2012). This effect is not always linear, with low to medium deer densities leading to higher plant species diversity because deer browsing increases vegetation structural heterogeneity and reduces interspecific competition among plants, whereas high densities of deer lead to high browsing pressure on all plant species and a homogeneous vegetation and reduced plant diversity. See, for example, results from a detailed study from temperate mixed forest in the Netherlands where browsing by deer (red deer, *Cervus elaphus* Linnaeus, 1758; roe deer, *Capreolus capreolus* (Linnaeus, 1758); fallow deer, *Dama dama* (Linnaeus, 1758)) led to non-linear changes in sapling density, soil compaction, and litter depth (Ramirez et al., 2021). Similarly, in a Canadian balsam fir forest inhabited by white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), aboveground biomass increased exponentially with decreasing deer density (Tremblay et al., 2006). Other studies, however, have shown that under certain conditions deer can promote the aboveground production of woody biomass in temperate regions, such as with the development of "browsing lawns": patches of the landscape where intense browsing activity increases the proportion of palatable species in the tree community (Churski et al., 2022; Cromsigt and Kuijper, 2011), or the development of dense branching in woody species as a response to chronic browsing pressure (Churski et al., 2022). Thus, deer may both reduce and increase woody biomass in the seedling and sapling layer, thereby influencing the carbon dynamics in these strata.

Deer can also alter the species composition of woody communities in forests, such as by influencing the balance between palatable and less-palatable tree species (Kuijper et al., 2010; Perea et al., 2014; Ramirez et al., 2021), particularly in the regenerating forest layer (i.e., seedlings and saplings). Ungulate browsing can also filter tree functional composition and diversity through the loss of species not tolerant to chronic browsing (Hedwall et al., 2018). These impacts on the regenerating forest layer can subsequently influence the forest canopy, affecting both the species composition of the canopy as well as stem density and canopy height (Reed et al., 2022). Such changes can have long-term effects on forest carbon sequestration (White, 2012), which are an important research avenue but beyond the scope of this study.

Deer-induced changes in species composition can affect carbon stocks by influencing the relative abundance of species that vary in wood density and carbon content (even if their effects on overall biomass are negligible; Martin et al., 2018). Wood density is an important trait for calculating aboveground biomass, and thus aboveground carbon stocks (Chave et al., 2005; 2009). Interspecific variation in wood density is not always included in large-scale studies quantifying carbon stocks (Myneni et al., 2001; Thurner et al., 2019, 2014) despite the potential for under- or overestimation of carbon stocks as a result of varying wood density among species (Chave et al., 2008; Clough et al., 2017; Laforest-Lapointe et al., 2014; Vannoppen et al., 2018). Further, carbon conversion factors

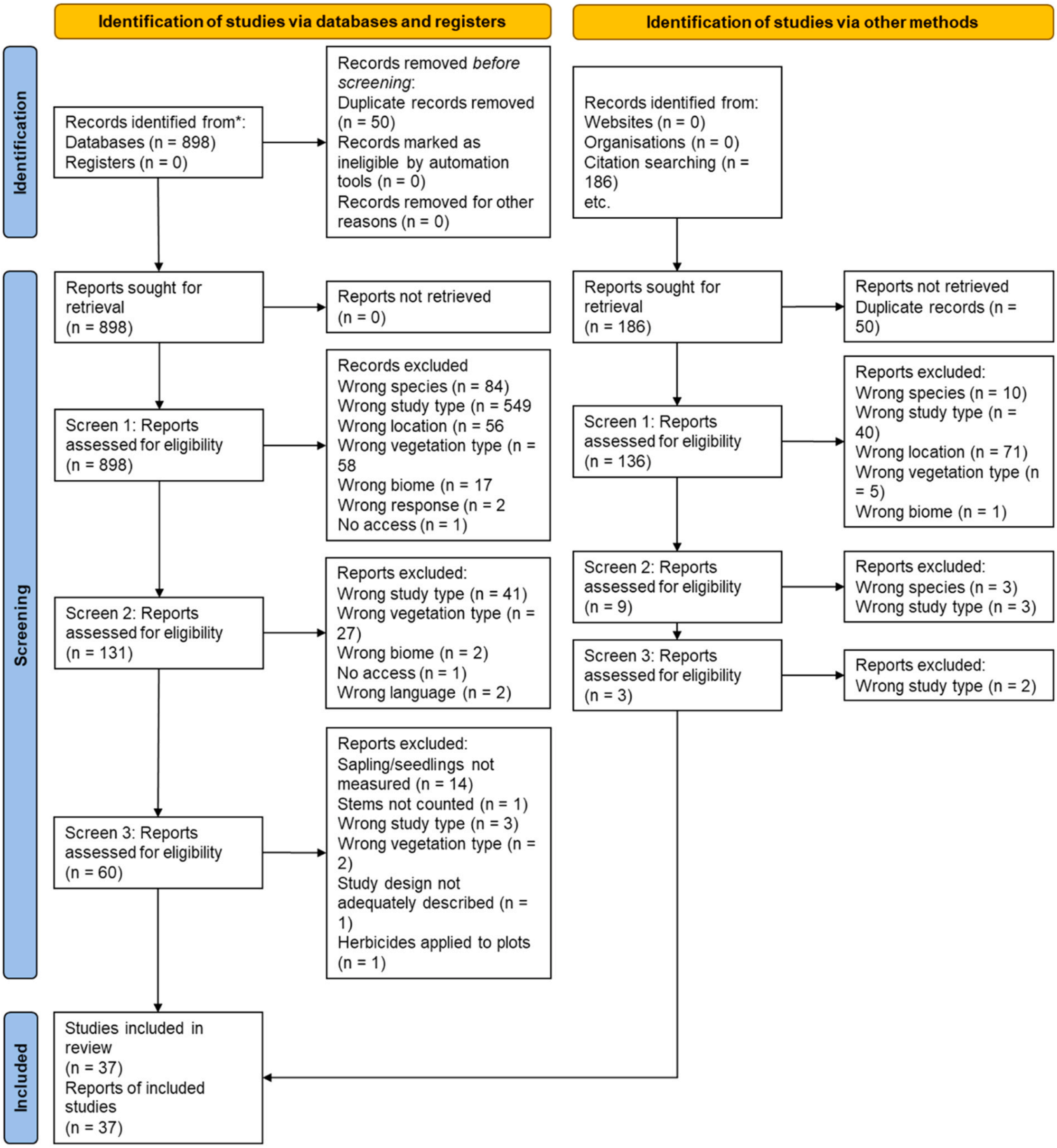

Fig. 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram (Page et al., 2021). Based on the template from Page et al. (2021). Screen 1 assessed titles and abstracts, screen 2 assessed the full text for moderators of interest (e.g., biome, vegetation type, whether it was an exclosure study), and screen 3 assessed if the study design was appropriate and whether variables of interest (e.g., stem height, stem density, diameter at breast height) were measured.

(CCFs) are needed to calculate aboveground carbon from aboveground biomass. Many studies use a CCF of 0.5 for all woody species or an average CCF by biome or tree type (i.e., coniferous vs. broadleaved) and do not account for interspecific differences (Aalde et al., 2006; Martin et al., 2018). Compiling CCF data from several databases for a large number of woody species, Martin et al. (2018) showed that CCF may vary widely among species and suggested that accounting for this variation is important for more precise assessments of aboveground carbon stocks in forests. The magnitude of the effect of deer-induced shifts in woody species composition on carbon stocks, particularly when considering interspecific differences in wood density or CCF, remains to be studied.

Thus, we identified two main knowledge gaps related to the potential impacts of deer on the aboveground carbon dynamics in the lower strata of temperate and boreal forests in Europe and North America. First, how do deer affect aboveground woody biomass and thereby carbon stocks in the seedling and sapling layer (individuals $\leq$ 3 m) of European and North American temperate and boreal forests? Second, how do potential deer-mediated changes in the tree community composition of the seedling and sapling layer influence aboveground carbon stocks?

We explored these questions through a systematic meta-analysis of experimental exclusion studies of common deer species in European and North American temperate and boreal forests. More specifically, we analyzed all experimental deer exclusion studies identified by our systematic literature search that provided empirical data which allowed us to compare aboveground biomass between deer exclusion and deer presence. From this, we estimated aboveground carbon stocks using two scenarios of wood density and carbon conversion factors: (1) a neutral scenario with no interspecific variation, assuming a single wood density value (the average across all species) and carbon conversion factor (0.5) for each species, and (2) a mean scenario using published mean wood densities and carbon conversion factors (CCFs) specific for each woody species. CCF reflects the proportion of wood consisting of carbon. The neutral scenario allowed us to explore how deer influence carbon storage via their effects on forest regeneration. Thus, this scenario only assessed the potential effects of deer on aboveground carbon through changes in the overall woody biomass of the seedling and sapling layer. By including species-specific trait values in the mean scenario, we investigated whether deer additionally affected aboveground carbon by changing woody species community composition in the seedling and sapling layer, that is, whether deer are shifting the community towards harder wood (higher wood density) species and/or species with higher carbon content.

2. Materials and methods

2.1. Literature search

2.1.1. General scope

We focused on the regenerating height class of woody plant communities in the seedling and sapling layer of European and North American temperate and boreal forests. The regenerating height class refers to seedlings and saplings within the browsing height of deer (maximum 3 m) (Nichols et al., 2015). Studies were limited to English and those published up to February 2021. Deer species were limited to those native to their study region: red deer (*C. elaphus*), roe deer (*C. capreolus*), fallow deer (*D. dama*) in Europe; and white-tailed deer (*O. virginianus*), mule deer (*Odocoileus hemionus* Rafinesque, 1817, including sub-species black-tailed deer and Sitka deer), and elk (wapiti; *Cervus canadensis* Erxleben, 1777) in North America. Moose (*Alces alces* (Linnaeus, 1758)) and reindeer/caribou (*Rangifer tarandus* (Linnaeus, 1758)) were considered native to both regions. Although exclosures can also prevent access to other large herbivores (e.g., wild boar, *Sus scrofa* Linnaeus 1758; domestic cattle, *Bos taurus* Linnaeus 1758; domestic sheep, *Ovis aries* Linnaeus 1758), only studies that attributed exclosure effects to deer were included in this meta-analysis.

2.1.2. Literature search and detailed selection criteria

We used Web of Science Core Collection (1900–2021) and Scopus (1960–2021) to conduct the literature search, following the PRISMA reporting standard (Haddaway et al., 2022; Page et al., 2021). The last searches were conducted on January 7 and February 2, 2021, to collect papers focused on Europe and North America, respectively. Two searches were conducted for each database and region, using either vernacular or Latin names for the deer species, biome type (boreal and temperate forest), exclosure type, and vegetation response variables as keywords in the search strings (see Supplementary Information A: Table S1 for details). In addition, we included studies from the bibliographies of major reviews on ungulate herbivory impacts on forest vegetation (Bernes et al., 2018; Forbes et al., 2019; Gardner et al., 2019; Ramirez et al., 2018; Redick and Jacobs, 2020; Tanentzap and Coomes, 2012), and one study following the suggestion of a co-author (Nopp-Mayr et al., 2020). We then conducted an eligibility assessment for all studies based on the eligibility criteria shown in Fig. 1. First, duplicates were identified and removed using the bibliometrix R package (Aria and Cuccurullo, 2017). A manual check indicated four false positives, which were also removed. The studies were screened by a single reviewer (KLO) in three steps. First, study titles and abstracts were excluded if they did not include any of the selected deer species, were not located in Europe or North America, did not study the biomes of interest (neither boreal nor temperate forest), were not exclosure studies, or did not study the effects of deer on regenerating seedlings and saplings in forests. Second, the full texts of the remaining studies were screened again for region, biome, presence of deer exclosures, whether target deer species impacts were distinguishable from other species, vegetation type (regenerating seedlings/saplings), and whether the study presented new empirical results (i.e., results were not obtained from simulations or another form of modelling). Disturbance type was also recorded during this step (e.g., logging, fires, insect outbreaks) but was not used as a selection criterion. Finally, for the publications remaining after step 2, we screened the full text of studies for the study design (i.e., if it contained information on plot and exclosure size, biome; whether planting of saplings/seedlings and other types of disturbances occurred) and whether the necessary variables were reported (stem density or species proportions, stem heights or height classes, total basal area or stem diameters, and summary statistics such as effect size and standard error). A risk of bias assessment was otherwise not conducted for individual studies (Page et al., 2021).

2.1.3. Data requests

The literature search yielded 898 unique records. After removing 50 duplicates, a further 136 records were included from the review bibliographies. 37 records remained after our selection steps, spanning a publication period between 2002 and 2021 (Fig. 1; Supplementary Information B). Excluded records can be found in Supplementary Information B. The corresponding authors of the 37 selected studies were contacted for their raw data and requested to provide the height and species of each individual seedling or sapling ≤ 3 m in a plot or subplot for both exclosure treatment and control plots. Authors were also asked to provide individual seedling and sapling diameters when available. Twenty-six responded, of which 12 provided 16 suitable datasets. A 17th dataset from Murphy and Comita (2021) was downloaded from the Dryad database (Murphy and Comita, 2020). In February 2024, two additional records were determined to have been missed in the final screening since 2021 (Asnani et al., 2006; Eschtruth and Battles, 2008), and their corresponding datasets were requested from the authors. At the time of submission, we did not receive data from Eschtruth and Battles

Table 1
Metadata for each case included in the meta-analysis and moderator analysis. The text in parentheses in the logging column indicates logging type. The text in parentheses under the conifer or broadleaf dominant forest column indicates the species that accounted for at least 50 % of the frequency of all seedling and sapling species present in the control plots. Cases that only had exclosures of the same age had a standard deviation (sd) of 0.

Dataset ID	Case	Continent	Biome	Dominant deer species	Logging	Planting	Conifer or broadleaf dominant forest	Average age of exclosure (years ± sd)	Metabolic weight density of dominant species (kg$^{0.75}$ km^{-2})
1	Kuiters and Slim (2002)	Europe	Temperate	Red deer	No	No	Conifer (*Pinus sylvestris*)	10.5 ± 0	74.24
2	Siipilehto and Heikkilä (2005)	Europe	Boreal	Moose	Yes (cleaning)	Yes	Broadleaf (*Betula pubescens*)	11.0 ± 0	93.73
3	Beguin, Pothier, et al. (2009a)	North America	Boreal	White-tailed deer	Yes (strip clearcutting treatment)	No	Conifer (*Abies balsamea*)	7.0 ± 0	201.33
4					No (strip closed-canopy forest)		Mixed (*Picea glauca* + *Betula papyrifera*)		
5	Beguin, Pothier, et al. (2009a)	North America	Boreal	White-tailed deer	Yes (shelterwood cutting treatment)	No	Conifer (*Abies balsamea*)	8.0 ± 0	201.33
6					No (natural closed-canopy forest)		Broadleaf (*Betula papyrifera*)		
7	Beguin, Prévost, et al. (2009b)	North America	Boreal	White-tailed deer	Yes (clearcutting areas)	No	Conifer (*Abies balsamea*)	7.41 ± 0.491	201.33
8					No (adjacent forest patches)			7.43 ± 0.496	
9	Kuijper et al. (2010)	Europe	Temperate	Red deer	No	No	Broadleaf (*Carpinus betulus* + *Acer platanoides*	7.0 ± 0	141.07
10	Ramirez et al. (2019)	Europe	Temperate	Roe deer	No	No	Mixed (*Pinus sylvestris* + *Betula pendula*)	4.04 ± 5.04	100.62
11	Parker et al. (2020)	North America	Temperate	White-tailed deer	Yes (overstory removal)	No	Broadleaf (*Acer rubrum*)	7.49 ± 0.779	134.24
12	Petersson et al. (2020)	Europe	Temperate	Moose	Yes (cutting canopy gaps)	No	Broadleaf (*Quercus robur/petraea*)	2.5 ± 0	51.17
13					No				
14	Perea et al. (2020)	Europe	Temperate	Roe deer	No	No	Broadleaf (*Ilex aquifolium* + *Prunus avium* + *Quercus pyrenaica*)	7.0 ± 0	65.86
15	Vuorinen et al. (2020)	Europe	Boreal	Moose	Yes (clear-cut)	Yes	Broadleaf (*Betula pubescens* + *Sorbus aucuparia*)	11.0 ± 0	82.97
16		North America				No	Conifer (*Abies balsamea*)	7.0 ± 0	157.31
17	Murphy and Comita (2021)	North America	Temperate	White-tailed deer	No	No	Broadleaf (*Prunus serotina* + *Fraxinus* sp. + *Hamamelis virginiana* + *Quercus montana*)	3.0 ± 0	0.507 – 1.09

(2008). The dataset from Asnani et al. (2006), received on February 24, 2024, did not include stem height data and was therefore unsuitable for inclusion in the meta-analysis.

As some studies reported results from more than one experimental design, we used 17 independent datasets (hereon referred to as cases) from 12 different publications for a two-stage Independent Participant Data meta-analysis (Table 1). An Independent Participant Data meta-analysis reanalyses the original dataset from each case, rather than analysing reported effect sizes (Stewart and Tierney, 2002). Each dataset was considered an independent participant. The moderators assessed in this meta-analysis are outlined in Table 1. As logging can affect the light conditions available to seedlings on the forest floor and affect their regrowth after browsing (Burton et al., 2021; Churski et al., 2017; Sabo et al., 2019), several datasets were split according to logging treatment when multiple treatments were applied (e.g., clearcut areas *vs.* closed-canopy forest areas).

2.1.4. *Data cleaning*

Sapling height measurements from the final year of sampling for each case were limited to the maximum height at which the largest deer species present browse (Supplementary Information A: Table S2). Species that tended to have a shrub-like growth form (i.e., not considered trees in this meta-analysis) were also excluded from the final dataset because it is difficult to estimate biomass (and thus aboveground carbon) for this growth form based on stem height and diameter alone. This included *Rubus* spp., *Lonicera periclymenum, Lonicera canadensis, Acourtia runcinata, Gaillardia arizonica, Lindera benzoin, Viburnum acerifolium, V. prunifolium x rufidulum,* and *Rosa canina*. Burn treatments were removed from the dataset of Petersson et al. (2020), and this dataset was then split between plots with and without tree-cutting treatments. Similarly, datasets from Beguin, Pothier, et al. (2009) were first separated between the strip clearcutting experiment and the shelterwood or partial cutting experiment, and then further divided between plots located in logging areas and plots located in adjacent closed-canopy forest. The same strategy was used for the dataset from Beguin, Prévost, et al. (2009), where data using plots in clearcut areas were analyzed separately from plots located within seed tree group patches, with plots subjected to a scarification treatment removed prior to analysis.

2.2. *Aboveground woody biomass and carbon calculation*

2.2.1. *Prediction of diameter at breast height*

All but two datasets used in the meta-analysis (Perea et al., 2020; Petersson et al., 2020) (Table 1) did not have complete field-measured diameter data available for every woody individual. The diameters of the partial datasets were modelled by fitting a linear mixed-effects model to the combined datasets from Perea et al. (2020) and Petersson et al. (2020), along with two studies that were not included in the meta-analysis but provided additional diameter data to this model: Churski et al. (2017) and Kolstad et al. (2018). Log-transformed diameter at breast height was included as a response, and log-transformed height and treatment were included as fixed effects, and case ID as a random effect to account for variation among cases. This full model was cross validated against a null model and models containing either log-transformed height or treatment as fixed effects using the k-fold method in package cv (Fox and Monette, 2025), where $k = 4$, clustered by case ID. The final model was selected based on the lowest mean squared error (Supplementary Information A: Figure S1). Model diagnostic plots were assessed and missing diameter data was predicted from existing height data for all partial cases using the predictmeans package (Luo, 2024). Model diagnostic plots can be found in Supplementary Information A (Figures S2-S3). The original diameter measurements were kept for Perea et al. (2020) and Petersson et al. (2020).

2.2.2. *Wood density and carbon conversion factor data*

Publicly available wood density data (trait ID #4, "Stem specific density (SSD) or wood density (stem dry mass per stem fresh volume)") were requested from the TRY Plant Trait Database (Kattge et al., 2020) on March 12, 2021 and released on May 28, 2021. In addition to wood density, aboveground carbon calculations require carbon conversion factors (CCF). We retrieved CCF for the species in our datasets directly from Dr. Martin (Martin et al., 2018). We used the wood density and CCF datasets to calculate mean wood densities and CCFs each woody species in the cases we selected for the meta-analysis. When stems were only identified to the genus, we used the genus mean. For species absent from the TRY or Martin et al. (2018) databases, we applied a commonly used generic value for CCF of 50 % (no standard error) (Martin et al., 2018) and/or a wood density of 0.58 g cm^{-3} (se $= 0.00$; mean of all species in the meta-analysis) for that species. Of the available data, 26.9 % of species had CCF measurements available and 98.7 % had wood density measurements available (Supplementary Information A: Table S3). The most common species in our global dataset were not necessarily the best represented in terms of trait data. Of the 20 most common species in the global dataset (defined as the proportion of stems out of total number of stems), 40 % ($n = 8$) had CCF measurements available and 75 % ($n = 15$) had WD measurements available (Supplementary Information B).

2.2.3. *Aboveground biomass*

The equation used to calculate aboveground biomass was selected based on the variables we both had access to and had *a priori* decided to include in our estimations of aboveground biomass (diameter, height, and wood density). The chosen equation was both suitable for smaller seedlings and saplings and included these variables. A resulting limitation was that the model was developed for trees in an unrelated study area (Iran) and not for coniferous species. Aboveground biomass (g) was calculated for each seedling and sapling stem in each case using height (m), measured or predicted breast height diameter (cm), and wood density (g cm^{-3}), according to Eq. 1 (Daryaei and Sohrabi, 2016).

$$AGB = 71.03(D)^{1.903} * H^{0.646} * wd^{0.571} + 112.72(D)^{2.258} * H^{-0.341} * wd^{1.377} + 11.71(D)^{1.810} \tag{1}$$

In Eq. 1, D is the diameter, H is the height, and wd is the wood density. Species-specific wood density values were used for the mean scenario, and the average wood density of all species in the meta-analysis for the neutral scenario.

2.2.4. Total aboveground carbon

Aboveground carbon stock (g) was calculated by multiplying the aboveground biomass of each stem in each case in the meta-analysis by a) its species-specific CCF in the mean scenario, and b) a generic CCF of 0.5 in the neutral scenario. The mean aboveground carbon stock values were calculated for each tree using the average species-specific CCF. Total aboveground carbon stock (g m^{-2}) was calculated by summing the aboveground carbon stocks across all tree individuals less than the maximum browsing height for deer species present per subplot (Supplementary Information A: Table S2) for each case in the meta-analysis separately. All further analyses were performed at the subplot level. We defined subplot as the smallest survey unit used in each case (e.g., a quadrat).

2.3. Meta-analysis

A two-stage meta-analysis was performed using R-package "metafor" v3.4.0 (Viechtbauer, 2010). In the first stage, a linear mixed-effects model (Bates et al., 2015) or linear model was fitted to each case with exclosure treatment (exclosure versus control) as the only fixed effect and aboveground carbon stock per subplot (g m^{-2}) as the response variable. Hereafter, datasets are referred to by their Dataset ID (see Table 1). Cases 2 −5, 7, 8, and 11 −17 were fitted with linear mixed-effects models where block was included as a random effect. Case 10 was fitted with a linear mixed-effects model where block and age were included as random effects. Cases 1, 6, and 9 were fitted with linear models as block was not available in their data. Cases 4 and 14 were also fitted with linear models as block did not account for any residual variation. Estimated effect sizes and standard errors were extracted from each model and compiled into a single data frame that was used to build second stage meta-analysis models for both the neutral and mean scenario using the rma.uni() function in metafor. The effect size measure was the raw mean difference (MD) in aboveground carbon stock per subplot (g m^{-2}) between the exclosure and control treatment groups. We used MD as this maintained the original measurement scale of cases outcomes and aided interpretation of the results. Effect sizes and associated standard errors per case were estimated in stage one of the meta-analysis using linear (mixed-effects) models, and a pooled effect size and associated standard error for all cases were estimated in stage two of the meta-analysis. Effect sizes were not standardised as all case outcomes were in the same units.

Random-effects meta-analysis models were used because individual cases differed significantly in terms of their location, biome, and dominant tree or deer species. A random-effects model reflects these differences and does not assume that all cases share an effect size. We used the REML method for these models, as it is suitable for continuous data (Langan et al., 2019; Veroniki et al., 2016). We used the Knapp and Hartung (2003) estimator, as it provides more robust estimates of variance compared to the default DerSimonian-Laird estimator, is less likely to lead to false positives, and is recommended for meta-analyses with a low number of cases (Higgins and Thompson, 2002).

2.3.1. Moderator analysis

Heterogeneity (I^2) is a measure of inconsistency between case outcomes and is presented as the percentage of variability in effect estimates that is due to heterogeneity rather than measurement error (Higgins and Thompson, 2002). Since the heterogeneity of the random-effects models was high for both scenarios ($I^2 > 50$ %), we performed a follow-up moderator analysis (Q_m) to determine if and what moderators (i.e., metadata from the cases) explained the heterogeneity among cases. Q_m is an omnibus test of moderators that assesses the overall significance of the model. A significant value indicates that there are differences between the moderator levels. We based the moderator selection on the metadata presented in the included cases and on what we expected to be ecologically relevant to either aboveground carbon stocks or deer effects. Thus, we initially included the biome (boreal or temperate), whether additional seedlings or saplings were planted (yes/no), logging status (yes/no), dominant tree type (gymnosperm vs. angiosperm, simplified into conifer vs. broadleaved), continent, total deer metabolic biomass (kg km^{-2}), dominant deer species, and average age of exclosures (years). Logging status included methods such as cleaning, shelterwood cutting, strip-cutting, overstory removal, gap removal, and clear-cutting. All moderators were taken as reported by the authors in their respective publications, except for the dominant tree species and tree type. We determined the dominant tree species for each subplot by summing the number of observations for each tree species in the control plots and taking the most common species. The dominant tree type was determined by calculating the cumulative frequency of each tree species (from most to least common) and determining whether gymnosperms (conifer) or angiosperms (broadleaf) dominated the study site (> 50 % of all trees). Cases were labelled as "Other" where neither was dominant. Only control plots were considered, as it was assumed that exclosure plots at initiation would be similar to control plots. It is important to note that the forest type in each case was determined by the seedling and sapling species compositions, and not by the overstory. The mature trees in each case may differ in composition from the seedling and sapling cohorts. Per case, deer biomass (kg km^{-2}) per species was calculated by multiplying local densities (n km^{-2}) (as reported by authors) by the average weight of adult male and female individuals found in literature (Supplementary Information A: Table S4). Species-specific biomass was reported for cases 1 and 10 and thus not recalculated. The total deer biomass was then converted to metabolic weight density (MWD) to standardise deer densities according to nutritional needs (Ramirez et al., 2018) using the formula: $MWD = mass^{0.75}$ (Kleiber, 1947). Total MWD of all species present was used in the moderator analysis. The species with the highest MWD was categorised as the dominant deer species for the moderator analysis. Deer density was not reported for case 15, and upon request, the authors suggested using county-specific deer densities estimated from hunting bags in Pennsylvania, US (Rushing et al., 2020). Because the county where the case was conducted was not included

(Westmoreland), we used the average maximum and average minimum deer densities from six of the eight surrounding counties (Indiana, Armstrong, Butler, Washington, Fayette, and Cambria).

The significance of each moderator was assessed using individual meta-regressions. Prior to analysis we determined whether each categorical moderator had a sufficient number of cases ($n \geq 5$) per level (Supplementary Information A: Table S5). Binary moderators that did not meet this requirement were removed (planting). Moderators with > 2 levels were reclassed so that all levels with fewer than 5 cases were combined into a single level, "Other". "Other" was included in all meta-regressions when relevant, but outcomes related to this level were not further assessed. Prediction intervals for overall scenario outcomes were calculated using the predict function in metafor. Sub-group prediction intervals were calculated using pred_interval_esmeans in orchaRd. Predicted effect sizes for continuous moderators (metabolic weight density and average exclosure age) were calculated for the average value of each moderator using the predict function in metafor. Per-case estimates were weighted using $1/SE_{case}$, i.e., precision. Post-hoc testing of significant categorical moderators was performed using Tukey's all-pair comparisons with single-step adjusted p-values in R package multcomp (Hothorn et al., 2016). Publication bias for moderator analyses with low across-case heterogeneity ($I^2 < 50$ %) were assessed visually using funnel plots. We did not find evidence of significant publication bias for any moderator (Supplementary Information A: Table S6, Figures S4-S5). All results were plotted using ggplot2 (Wickham et al., 2024) and orchaRd (Nakagawa et al., 2023). Results tables were constructed using modelsummary (Arel-Bundock, 2024), kableExtra (Zhu, 2024), and flextable (Gohel and Skintzos, 2024). The dataset used for analysis is archived at https://doi.org/10.5281/zenodo.13619198.

3. Results

On average, across all cases, there was no significant, consistently positive or negative impact of exclosures on aboveground carbon per subplot in the mean or neutral scenario, and effects of individual cases varied widely (Table 2, Fig. 2). Differences between the two scenarios were minor (Fig. 2). Individually, four cases (3, 5, 8, 10) showed a consistent increase in aboveground carbon following deer exclusion across both scenarios, with substantial variation in outcomes. The average MD across the four cases in both scenarios was 321 ± 465 g C m^{-2}, compared to a minimum MD of 46.31 g C m^{-2} (case 5, mean scenario), and maximum MD of 1130.71 g C m^{-2} (case 3, mean scenario). Only one case (17) showed a reduction in aboveground carbon following deer exclusion across both scenarios (Fig. 2), though the difference between control plots and exclosure plots in this case was very small in both scenarios ($MD = -1.33 \pm 0.00$ g C m^{-2}). Six cases had non-significant outcomes in both the original case and in this meta-analysis. One had significant positive outcomes in both. four case outcomes did not match between the original case and this meta-analysis (i.e., the effect of deer on stem density was not the same as the effect of deer on aboveground woody carbon). The remaining six cases did not originally report the effects of deer exclusion on stem density.

In both scenarios, among-case heterogeneity was considerable (Table 2). The moderator variables biome, metabolic weight density, average exclosure age, dominant deer species, continent, and logging were not significant in any scenario (Supplementary Information A: Table S7). Dominant tree type was a significant moderator for both scenarios, indicating that there was a significant difference between moderator levels (Mean: $Q_m = 7.53$, $p_m = 0.02$; Neutral: $Q_m = 11.88$, $p_m = 0.001$; Fig. 3a–b). In both scenarios, overall, there was a small, but significant negative effect of deer exclusion in broadleaf-dominated cases, and significant positive effect in conifer-dominated cases (Supplementary Information A: Table S7).

4. Discussion

We hypothesised that, by influencing tree species composition and the relative abundance of species with different wood density or CCF, deer may affect aboveground carbon stocks even if they do not change aboveground biomass. However, we found that the direction and size of the effects of deer exclusion on aboveground carbon stocks were similar for both the neutral and mean wood density and CCF scenarios. Across-scenario differences were only apparent in case 16, where the effect of deer exclusion was found only in the neutral scenario. However, as boreal forests generally have a higher proportion of coniferous species than temperate forests, the effect of biome may simply be an artefact of that. The lack of species-specific CCF data for many of the species included (see Supplementary Information A: Table S3) may result in an underestimation of across-scenario differences. More than 70 % of tree species included in our analyses lacked data on CCF and were assigned a generic CCF of 0.5. As such, our ability to test whether using CCFs was

Table 2
Overall meta-analysis outcomes for the mean and neutral scenarios. MD is the estimated raw mean difference in aboveground carbon (g m^{-2}) between control and exclosure plots. Positive values indicate an increase in aboveground carbon in exclosure plots relative to controls. Bolded Q values indicate that the differences between cases are not caused by chance ($p \leq 0.05$). I^2 is an estimate of the relative heterogeneity across cases, measured in percent. An $I^2 > 50$ % is considered high heterogeneity, indicating that some other factor is contributing to heterogeneity across cases.

	Mean	Neutral
MD	27.39 [−7.14, 61.92]	34.03 [−6.76, 74.82]
I^2	58.16	72.64
τ^2	678.56	1381.67
df	16	16
Q	**54.91 (p < 0.001)**	**64.20 (p < 0.001)**

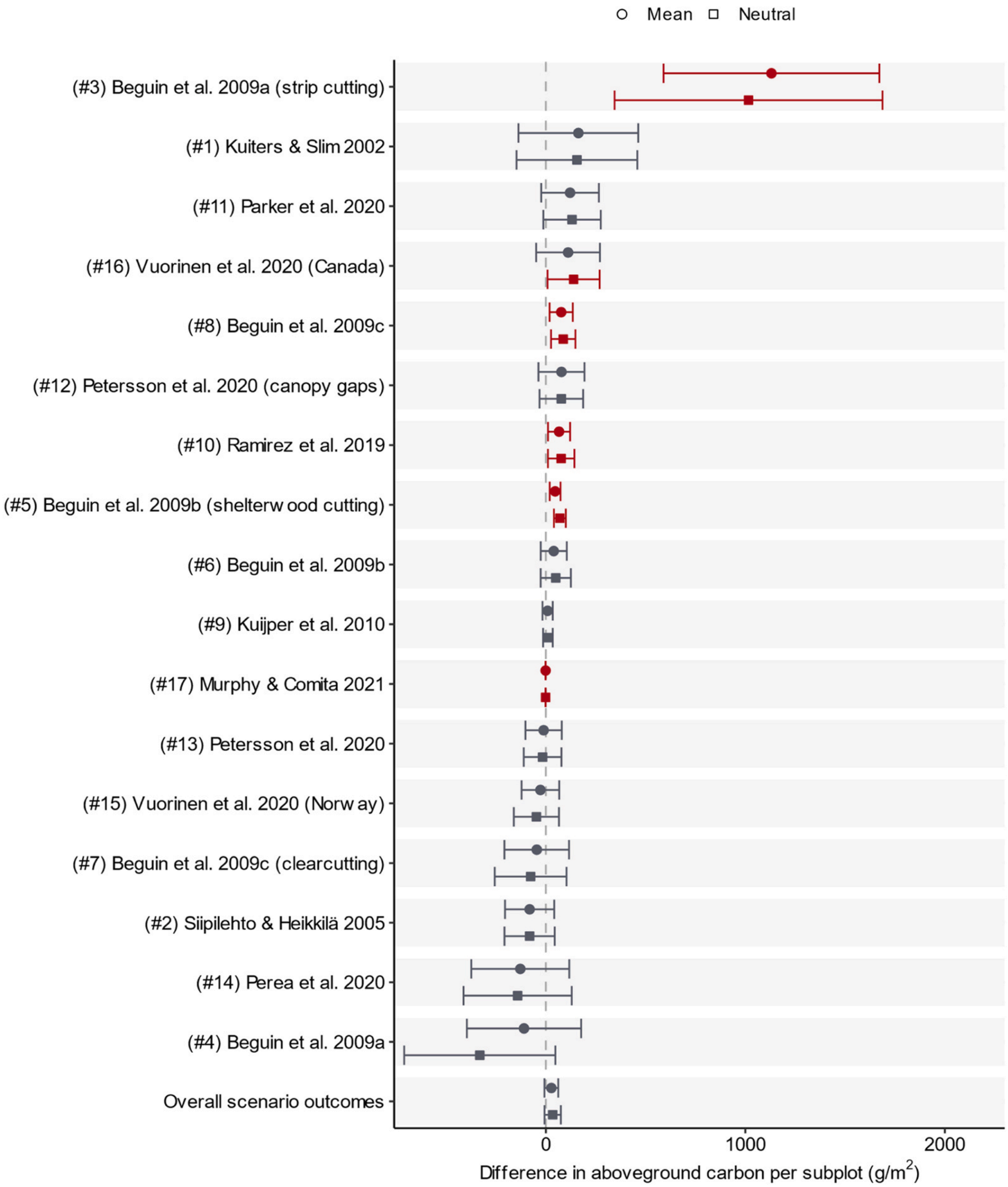

Fig. 2. Summary of mean and neutral meta-analysis scenarios of aboveground carbon responses to deer exclusion. For each case, points represent the estimated effect size of each case and lines represent the respective 95 % confidence intervals. Scenarios are indicated by point shape: mean = circle, neutral = square. The last row shows the overall meta-analysis outcomes per scenario, where points represent the mean effect size of all cases and bars the 95 % confidence intervals. The observed outcome was the difference in aboveground carbon per subplot (g m^{-2}) between the exclosures (deer absent) relative to the controls (deer present). Positive values indicate an increase in aboveground carbon when deer are excluded, and the reverse for negative values. 95 % confidence intervals that do not cross the 0 line represent statistically significant effects ($p < 0.05$) and are coloured red. Non-significant outcomes are coloured dark grey. Estimates are grouped by case and scenario, then ordered by the observed outcomes. Study IDs are shown in parentheses next to case names.

appropriate was likely limited by our largely incomplete CCF dataset. However, while overall CCF data was lacking, CCF data was available for 40 % of the twenty most common species in our data set (by stem number), including the three most common species (*Abies balsamea, Pinus sylvestris,* and *Fagus sylvatica*) (Supplementary Information B: Trait metadata). This suggests that there may be relevant, though potentially still underestimated, differences in species-specific CCF and wood density between conifer- and broadleaved-dominated forests. Further, the equation used to calculate aboveground biomass (Eq. 1) does not account for different growth forms or branching density that can result from deer browsing (Churski et al., 2024, 2022). As a result actual aboveground biomass may be higher than calculated in the presence of deer, and therefore our estimates of aboveground biomass, and the effects of deer, are relatively conservative. Though Eq. 1 is based on small-diameter saplings in a temperate forest and as such is likely more

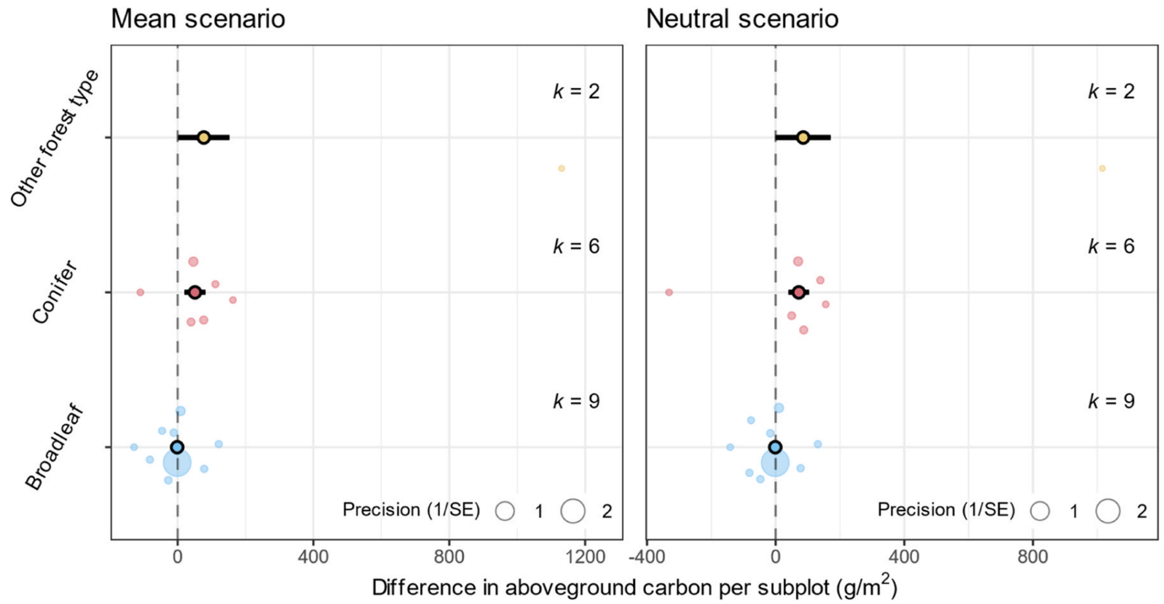

Fig. 3. Orchard plots showing mean effect sizes and 95 % confidence intervals (thick line), and 95 % prediction intervals (thin line) for each level of the moderator biome (a, b) and dominant tree type (c, d), with each scenario visualised separately. The observed outcome was the difference in aboveground carbon per subplot (g m-2) between the exclosures (deer absent) relative to the controls (deer present). Positive values indicate an increase in aboveground carbon when deer are excluded, and the reverse is true for negative values. 95 % confidence intervals that do not intersect the 0 line represent statistically significant effects ($p < 0.05$). 95 % prediction intervals estimate the range wherein potential true effects could fall and represent the dispersion of effect sizes across cases. Per-case estimates are shown as circles, with their size indicating the weighting of each case (1/SE), i.e., precision. k = the total number of cases per moderator level.

suitable than more commonly available biomass equations based on mature tropical forests, it is limited by the species modelled (all broadleaved). As such, it may not generalise well outside of its original context, especially for coniferous species.

It has become increasingly evident that the effects of growing deer populations and their expanding distribution across the northern hemisphere on forest regeneration are often variable and context dependent (Pringle et al., 2023). This reflects a more general pattern found for other taxa in other ecosystems. Trepel et al. (2024) found that while large herbivores generally cause a decrease in plant biomass, there was a wide variety of effects reported across studies and environments. Our results highlight this complexity: in both the mean and neutral scenarios, we found no evidence of a consistently positive or negative effect of deer exclusion on aboveground woody carbon estimates in the seedling and sapling layer (i.e. tree saplings up to and including 3 m) across all sites. Meta-analysis outcomes were not consistent even for those located in the same geographical and ecological context (i.e., Cases 3, 5, and 8 versus cases 4, 6, and 7, all located on Anticosti Island, Quebec, Canada), nor consistent with original case outcomes on the effects of deer exclusion on tree stem density (Supplementary Information A: Table S8; see Supplementary Information B: Study outcomes for outcomes of other response variables). The presence of meta-analysis case outcomes that did not match original case outcomes suggests that an increase in the number of saplings and seedlings due to deer exclusion does not necessarily translate to an increase in aboveground wood carbon, and vice versa. This difference may be due to our method of estimating aboveground carbon stocks, which incorporated both stem height and diameter at breast height. For example, release from browsing pressure can result in an increase in average stem heights within exclosure plots, leading to higher aboveground carbon stocks even if stem densities are the same as in control plots (Nosko et al., 2020).

We found that the moderators total metabolic weight density (MWD) and average exclosure age did not explain across-case heterogeneity in either scenario. Landscape-level forage availability, local forestry activities, and their interaction, could explain why high MWD did not consistently result in positive effects of deer exclusion (Pfeffer et al., 2021). Outcomes were highly variable in cases that had a MWD > 115 kg km^{-2} (Ramirez et al., 2021). Of these, three showed significant effects of deer exclusion and where the case site was also logged before or during the experiment. Logging may increase landscape-level forage availability, where it opens canopies and reduces light limitation on the seedling and sapling layer, potentially facilitating the regeneration of food plants (Sabo et al., 2017). When forage availability is high, even high deer densities may not exert significant pressure on the regenerating forest layer (Royo et al., 2017). Conversely, low forage availability may result in increased browsing pressure on non-excluded, cut plots where forage in the form of regenerating plants was more readily available (Miller et al., 2010). However, there are always exceptions: MWD was high in case 7 (201.33 kg km^{-2}) and plots were clearcut prior to the experiment, yet there was no clear effect of deer exclusion on aboveground carbon stocks.

We did not find a significant effect of exclosure age in either scenario. In our meta-analysis, the average exclosure age ranged from 2.5 to 11 years (mean = 7.8 ± 2.81). Thus, our results only reflect the short-term effects of deer exclusion on the seedling and sapling layer ($\leq$ 3 m), and the long-term effects on vegetation structure or species composition, but also carbon storage, need further study

(Tanentzap et al., 2012). This highlights a gap in our knowledge on the long-term effects of deer exclusion, particularly given the temporal scale on which forests develop compared with the age of exclosure studies (Newman et al., 2014; White, 2012).

There were no differences in the effectiveness of deer exclusion found between temperate and boreal biomes. Previous studies have also found that biome, and measures related to biome (e.g., Net Primary Productivity), did not moderate the effects of herbivory, supporting the idea that the effects of deer herbivory may be more site-specific rather than governed by large-scale contexts (Jia et al., 2018; Koerner et al., 2018). However, it is important to note that moderator analyses are limited in power and struggle to detect small differences between sub-groups (Cuijpers et al., 2021). Thus, we cannot say with certainty that there are no differences in deer effects on aboveground carbon stocks between different levels of the assessed moderators.

Dominant tree type was the most consistent moderator, with overall significant effects on aboveground carbon stocks differing between conifer- and broadleaf-dominated cases found in both scenarios. We found a pattern of small negative effects of deer exclusion on aboveground carbon stocks in broadleaf-dominated cases, and larger, positive, effects in conifer-dominated cases. Study sites dominated by coniferous seedlings and saplings showed a much more marked response to deer exclusion, possibly due to an increase in regenerating broadleaved trees at these sites following deer exclusion (Kolstad, Austrheim, Solberg, Venete, et al., 2018). The negative effect of deer exclusion in cases dominated by broadleaved seedlings and saplings could be due to deer browsing inducing increased branching in broadleaves within control plots (Churski et al., 2022; Cromsigt and Kuijper, 2011). Increased branching produces a "cage" that can protect stems from browsing or reduce browsing pressure on individual shoots, allowing saplings to eventually outgrow the browsing zone of deer (Churski et al., 2022) and potentially resulting in higher aboveground carbon stocks in control versus exclosure plots.

5. Conclusion

Deer may play a significant role in biogeochemical cycles through indirect processes, for example by influencing the amount of plant biomass in the system (Schmitz et al., 2014), however the impacts of deer on regenerating forest carbon are driven by mechanisms whose identities are not yet fully evident. In this meta-analysis we show that the effects of deer exclusion on aboveground woody carbon stocks in the seedling and sapling layer ($\leq$ 3 m) of European and North American forests were variable and context-dependent. Most cases presented inconclusive effects of deer exclusion on carbon stocks, and 35 % of reviewed cases showed positive effects (i.e., increased carbon storage inside deer exclosures). Yet despite the short duration of all cases, as well as the high variation in effect sizes between cases, we still found a small difference between coniferous- and deciduous-dominated forest systems, highlighting the need for future research into the mechanisms driving this difference. Future exclosure studies should explicitly include aboveground carbon stock estimations and we encourage revisiting existing exclosures to more accurately assess the impacts of long-term deer exclusion on vegetation recovery. We again stress the short-term nature of the included exclusion studies, 2.5–11 years on average, and the importance of studying effects of deer at much longer timescales. We also recommend studying exclusion effects as a function of multiple, potentially interacting, moderator variables (such as biome and forest type, but also landscape-level forage availability, canopy openness, and ecosystem productivity), as it is unlikely that a single driver mediates this relationship (Ramirez, 2021). Future meta-analyses could benefit from utilising multivariable meta-regression models, though low statistical power remains an issue when few studies are available for inclusion. A comprehensive global analysis including other regions and their native species (i.e., South America, Asia, and Northern Africa) would be a valuable avenue for future research, as it would increase the overall sample size and provide insights into whether deer impacts are similarly variable across the world. As such, we urge the development of collaborative field studies that implement standard experimental designs and protocols that measure not only the forest regeneration on the lower strata, but also other components of aboveground carbon stocks (e.g., herbaceous and shrub layers), the long-term effects on higher forest strata (such as mature canopy trees), and the inclusion of other regions and deer species, to assess the impacts of deer exclusion on aboveground carbon storage more accurately.

Funding

No funding was received to assist with the preparation of this manuscript.

CRediT authorship contribution statement

Klara Leander Oh: Conceptualisation, Formal analysis, Writing – Original Draft, Visualisation. **Gunnar Austrheim:** Investigation, Writing – Reviewing and Editing. **Julien Beguin:** Investigation, Writing – Reviewing and Editing. **Marcin Churski:** Investigation, Writing – Reviewing and Editing. **Steeve D. Côté:** Investigation, Writing – Reviewing and Editing. **Anders L. Kolstad:** Investigation, Writing – Reviewing and Editing. **Dries P.J. Kuijper:** Investigation, Writing – Reviewing and Editing. **A.T. (Loek) Kuiters:** Investigation. **Jeffery L. Larkin:** Investigation, Writing – Reviewing and Editing. **Stanisław Miścicki:** Investigation, Writing – Reviewing and Editing. **Halie A. Parker:** Investigation, Writing – Reviewing and Editing. **Ramón Perea:** Investigation, Writing – Reviewing and Editing. **Linda K. Jensen:** Investigation, Writing – Reviewing and Editing. **Bogumiła Jędrzejewska:** Investigation, Writing – Reviewing and Editing. **Juan Ignacio Ramirez:** Investigation, Writing – Reviewing and Editing. **Jouni Siipilehto:** Investigation, Writing – Reviewing and Editing. **Pieter A. Slim:** Investigation, Writing – Reviewing and Editing. **Jean-Pierre Tremblay:** Investigation, Writing – Reviewing and Editing. **Laurent De Vriendt:** Investigation, Writing – Reviewing and Editing. **Katariina E.M. Vuorinen:** Investigation, Writing – Reviewing and Editing. **Mariska te Beest:** Conceptualisation, Supervision, Writing – Reviewing and Editing. **Joris P.G.M. Cromsigt:** Conceptualisation, Supervision, Writing – Reviewing and Editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03961.

Data availability

Research Link Provided

Context-dependent effects of deer on aboveground carbon stocks in the regenerative tree layer in temperate and boreal forests: a meta-analysis (Zenodo)

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