

Monitoring deer food and browsing in forests: Coherence and discrepancies between national and local inventories

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ABSTRACT

Field-based monitoring of deer food availability and browsing on recruiting forest trees is a necessary but labour-intensive task. We explored how such estimates from a low-resolution multipurpose national forest inventory (NFI) (plot density 0.3 km^{-2}) corresponded with estimates from local inventories that specifically and in greater detail monitor the availability of deer food and browsing intensity (LFI) (plot density $2\text{--}3 \text{ km}^{-2}$).

We used NFI and LFI data from 16 moose *Alces alces* ranges (mean area $276 \pm \text{SE } 69 \text{ km}^2$) in southern Norway. Only the height segment 30–130 cm of browsable trees could be obtained from the NFI data, while moose can browse trees from 30 to 300 cm in height. According to the LFI, the browse species did not have similar proportions of their browsable stems below 130 cm. Using only the stems from heights of 30–130 cm overestimated the availability of RAS (rowan, aspen and sallow) relative to birch (silver birch and downy birch) and Scots pine.

The browsable biomass per stem of each species also varied between ranges, which introduces uncertainty to the food availability estimates that are based on stems only. Nevertheless, the NFI density of stems at 30–130 cm heights can be a useful index for species-specific comparisons of browse availability across ranges, because the variations between ranges in stem densities outweighed the biomass variations per stem. The NFI and LFI estimates of the species-specific densities of stems at 30–130 cm heights were significantly related and close to isometric (1:1), especially for RAS and pine.

We did not find strong relationships between NFI and LFI in the browsing intensity (i.e. proportion of shoots that were browsed during the winter). The explained variation was only 11% (R^2) for RAS ($p = 0.281$) and 32% for pine ($p = 0.028$). This was likely due to the small sample sizes of browsed trees in the NFI and methodological differences between the NFI and LFI in how browsing intensity is estimated.

Conclusions: Using data from national forest inventories can be an efficient but low-resolution way to monitor browse availability for deer, provided that the monitoring includes the full range of tree heights reachable for the deer (e.g., 30–300 cm for moose). It is also a prerequisite that the number of NFI plots is sufficient to cover the spatial variability of the area. Regarding browsing intensities, adjustments in both the NFI and LFI approaches are needed to make the two monitoring schemes more comparable.

1. Introduction

To monitor deer food availability and browsing on recruiting forest trees, we need methods that are cost-efficient yet still have sufficient spatial resolution. This is especially challenging for wide-roaming animals, whose vast habitats are becoming ever more heterogeneous due to the accelerating fragmentation caused by human activities (Fischer and Lindenmayer, 2007). Fragmentation typically increases spatial variations in habitat quality and causes nutritional limitations for per-severing animals (e.g., Garel et al., 2007; Allen et al., 2017, but see also

Harveson et al., 2007). The increased spatial variations reinforce the need for cost-efficient monitoring, because more area needs to be sampled.

The main challenge for the monitoring of food for deer is to make the effort simple but yet capture enough of the intricacies of plant growth forms and animal feeding behaviours. The amounts of edible biomass per food item vary strongly among plant species and even with local conditions for the same plant species (Wam et al., 2010; Monteith et al., 2014). The *acceptability* of the biomass to deer may also vary with location, because plant individuals growing in different areas can have

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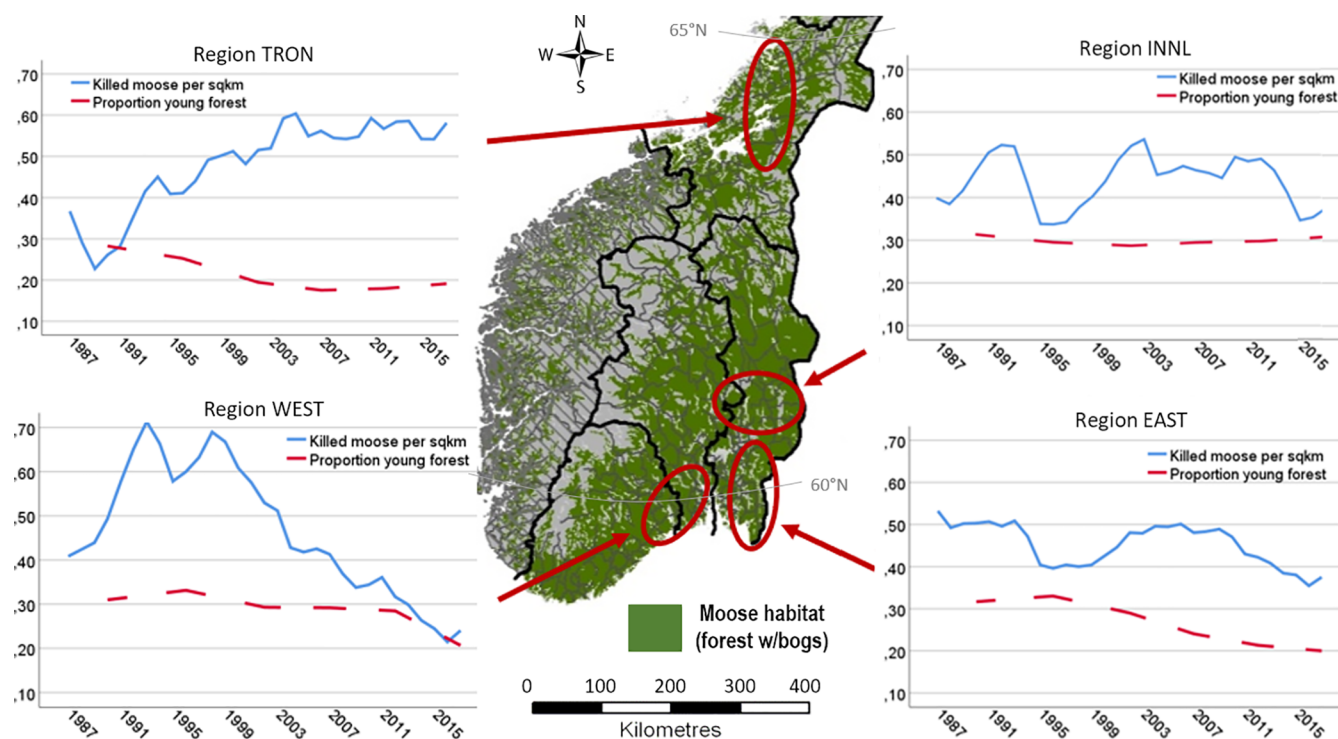


Fig. 1. Time series of moose harvests (animals/km²) and proportions of young forests in four regions of southern Norway. The proportion of young forest is an index of food availability for moose. Here, it comprises forest stands in development classes I-II with trees up to 13 m mean height, depending on the site index (Stokland et al., 2003).

different nutritional contents (Wam et al., 2018). All of these factors may be inherent to sites or may have been acquired as a result of past browsing history (Stolter, 2008; Royo et al., 2010; Speed et al., 2013; Pastor, 2016; Russell et al., 2017; Petersson et al., 2019). It is impossible to capture much of these variations in cost-efficient monitoring, especially at larger spatial scales. Most estimates of food availability for deer therefore explain only a part of the variations in the realized food value across landscapes, as expressed in terms of animal fitness (e.g., Herfjald et al., 2014). Local conditions must always be considered and data should only be extrapolated across areas with similar foodscapes (*sensu* Searle et al., 2007).

At present, monitoring of nature is increasingly carried out by using remote sensing. Food availability for deer, for example, has been monitored by using indices based on the spectral reflections from photosynthetic activity in the landscape (mainly NDVI, Pettorelli et al., 2005) and/or vegetation structures derived from LiDAR (Schaefer and Lamb, 2016). Remote sensing is promising for monitoring variations in food availability in habitats with fairly uniform vegetation (e.g., Hamel et al., 2009), but the methods still appear to have insufficient resolution for more heterogeneous habitats such as forests (Boan et al., 2013; Borowik et al., 2013), at least without accompanying ground-based field data (Lone et al., 2014; Melin et al., 2016). Hence, to acquire adequate estimates of food availability and browsing in such habitats, ground-based field inventories will likely remain necessary. The question is, how can we extend the sampled areas without increasing costs or losing too much precision?

In this study, we compared large-scale low-resolution data from the National Forest Inventory of Norway (hereafter NFI) with local high-resolution data from specialized food inventories for forest-dwelling deer (hereafter LFI). The NFI covers the entire forested area of Norway with a sample plot density of 0.3 km⁻² for most of the forested area. For a more detailed outline of the NFI design, we refer to Breidenbach et al. (2020). The LFI has approximately ten times the plot density (2–3 km⁻²), but covers far less land. National forest inventories are available in most countries that have extensive forest resources (Vidal

et al., 2016). Utilizing these regularly conducted inventories could be an efficient and structured way to monitor deer food availability and browsing in forest environments. Given both the aspirations and the constraints outlined above, we explored whether the NFI and LFI convey similar information on deer food availability and browsing intensities.

We focused on woody species (i.e. browse) which constitute the staple food for moose, *Alces alces*, during winter (Wam and Hjeljord, 2010). We used NFI and LFI data from 16 moose ranges in four forest regions of southern Norway having distinct historic and ecological conditions for moose. Because the NFI and LFI inventories have different objectives, they do not collect data on browse at the same level of detail. The NFI records the density of browsable stems in height segment categories and the proportion of shoots on these stems that were browsed during the previous winter. The LFI records stem densities combined with their mean stem heights for the plot. It also records the proportion of browsed shoots, and the number and length of unbrowsed shoots, which can be used to estimate the available browsable biomass per tree and per unit area. From the LFI data, we tested the relationship between stem density and browsable biomass and predicted a positive isometric (1:1) relationship within each tree species. Next, we tested the relationships between NFI and LFI regarding 1) stem densities and 2) browsing intensities. Again, we predicted positive isometric relationships.

2. Methods

2.1. Study area

The study area covers four forested regions in the southeastern and middle parts of Norway. All are situated in the boreal vegetation zone (Moen 1999) where the forest is dominated by Norway spruce (*Picea abies* L. Karst), Scots pine (*Pinus sylvestris* L.) and birch (*Betula* spp.) with other deciduous species interspersed at varying tree densities. In forest stands dominated by spruce, tree harvesting is mainly performed

Table 1

Forest characteristics (% of forested area) and climatic conditions¹ in four forested regions of southern Norway. Forest characteristics estimated from the large-scale National Forest Inventory (NFI) compared to estimates from local inventories of deer browsing (LFI).

	WEST region		EAST region		INNL region		TRON region	
	NFI	LFI	NFI	LFI	NFI	LFI	NFI	LFI
Forest stage structure ² :								
Within browsing height	12%	8%	12%	8%	14%	12%	8%	8%
Above browsing height	88%	92%	88%	92%	86%	88%	92%	92%
Bogs	5%	3%	7%	7%	7%	5%	20%	13%
Growing season (days)		170		176		153		155
Temperature sum		1088		1178		901		743
Annual precipitation (mm)		1056		811		771		1294
Mean altitude (m.a.s.l.)		282		186		415		273

¹ Climatic data are 30-year normals from 1981 to 2010 which were provided by the Norwegian Meteorological Institute (Lussana et al., 2016).

² Within browsing height of moose = dominant tree height of forest stand < 4 m (class I and 40% of II in the NFI development class system). Above browsing height is > 4 m (NFI classes III-V and 60% of II). We used 4 m as the delimiter which is higher than the upper browsing height of moose (3 m) because stands are uneven in height. A stand with a mean height of 4 m may also have several trees < 3 m.

by clearcutting at the commercially mature stage and the harvested areas are usually regenerated by planting within 1–2 years. Pine stands are normally harvested and regenerated by the seed tree method. The clear-cuts in Norway are small when compared to clear-cuts elsewhere (i.e. median 2.1 ha in spruce forests and 4.0 ha in pine forests) (Granhus and Eriksen, 2017).

The four regions differ in regard to their historic moose populations and forest development (Fig. 1) and in their current forest age structures, altitudes and climates (Table 1). Within each forested region, we obtained data from 2 to 7 LFI inventories that each covered a distinct moose range. Moose ranges are delimited by major landscape barriers such as infrastructure, large water bodies or mountains. They largely correspond to moose management units and so may have different historical management regimes.

The areas included in our study covered all forested land, woodland and bogs below the tree line (using 800 m a.s.l. as the cut-off for all regions) which varied from 77 to 1267 km² (mean 276 ± 69 SE km²) between moose ranges and from 3626 to 11,750 km² (mean 7576 ± 1517 SE km²) between forest regions (the area of a region only includes areas of study ranges within that region). The meteorological data in Table 1 are averages for the period from 1981 to 2010 and were extracted from a 1 × 1 km climate grid which was established by interpolation of measurements from meteorological stations operated by the Norwegian Meteorological Institute (Lussana et al., 2016). The lengths of the growing season and temperature sums were calculated using a threshold of +5 °C.

2.2. Data from the national forest inventory (NFI)

The NFI plots are 250 m² in size and were established at each intersection of a 3x3 km grid across the major forested parts of the country. Each plot is resampled every 5th year with 1/5 of all NFI plots visited each year over a 5-year cycle. Plots from each part of the country are included each year, so there should be a negligible year-area bias (for a more detailed description of the sampling design, see Breidenbach et al., 2020). In this study, we mainly used data collected from 2010 to 2014.

The relevant data collected in the NFI consist of site productivity (site index), forest stand ages and development classes, species-specific stem densities within height segments (more on this below), and proportions of shoots from the previous summer that were lost to deer browsing in winter (a photo manual of browsing signs is given in Viken, 2017). The NFI measures the site index based on the age and height of the largest (by using the diameter at breast height (DBH) = 1.3 m above ground) individuals of the dominant tree species in a tree stand (typically spruce, pine or birch) (the H40-system, Tveite, 1977) and is essentially an index of tree growing conditions. An H40 value of 17, for

example, indicates that the dominant trees in the site may grow to 17 m in height 40 years after reaching a height of 130 cm. The site index depends on soil fertility, moisture and local climate. For this study, we grouped the NFI plots into four site index classes to make them comparable with the site index classes used by the LFI: high (H40 ≥ 17), intermediate (H40 = 11–14), low (H40 < 11), and impediment. Here, impediment includes unproductive forestland with a potential yield capacity of < 1 m³ wood produced per ha and year and bogs with and without trees. Productive forest is further classified into five development classes based on age and site index. Class 1 consists of recently harvested stands, class 2 consists of stands with established regeneration, classes 3 and 4 consist of stands at early and late thinning stages, respectively, whereas class 5 consists of commercially mature forest. For an explanation of what these classes mean in terms of typical ages and heights of forest stands, see Stokland et al. (2003).

The NFI tallies stems with browsing value to deer in four circular subplots of 5.3 m² (total 21.2 m²). Stems below 30 cm are not counted because they are rarely browsed in winter as they are typically covered by snow. In the field, the stems are categorized into three size classes, of which only one (stem height 30–130 cm) is fully within the browsing height of moose and is therefore useful for this study. The NFI currently groups tree species into four classes, of which three are comparable with the LFI: (1) Scots pine *Pinus sylvestris*; (2) RAS = rowan *Sorbus aucuparia*, aspen *Populus tremula* and tree-forming willows, *Salix* spp.; and (3) birches, *Betula* spp. The proportions of shoots that have been browsed in winter by deer (mainly moose in our study areas) is recorded for each group.

2.3. Data from local inventories of deer food (LFI)

The LFI data stem from field inventories conducted on 16 separate moose ranges in single years throughout the period from 2005 to 2016. All inventories were carried out during the peak of the growing season (June–July). We have published elsewhere a detailed field-work protocol (Wam et al., 2010). In the LFI, circular plots of size 12.5 m² (r = 2.0 m) are systematically distributed every 15 m (paced off by steps) along straight transects in young recruiting forest stands (see below) and every 75 m in the remaining area of the forest (including bogs with or without trees). In the 16 LFI inventories used in this study, there were 17 ± 1.1 transects per range (mean ± SE). We systematically distributed transects across the landscape on maps prior to the fieldwork with the aim of obtaining a representative sample of the entire forest. Transects were either distributed in parallel and separated by an even distance (on fairly flat ranges) or were stratified to capture altitudinal gradients (in more elevated ranges). On one range (Salbruket), the transects were less systematically distributed (to test a new setup). Within the largest range, Ringsaker, most transects were

angled to make stratification across gradients more cost-efficient.

Tree data from the LFI plots used in this study consist of species-specific stem densities and their plot-representative stem heights, numbers of unbrowsed shoots with current annual growth (CAG) per stem, numbers of browsed shoots and CAG lengths (measured to the nearest cm) per unbrowsed shoot. All stems on the plot are counted if at least parts of their crowns are within the height interval 30–300 cm. Stem parameters are measured on one sample stem that is considered to be representative of the plot with regard to plant growth vigour (i.e. tree height and crown volume) and deer browsing intensity (Wam and Hjeljord, 2020).

To make plant species groups comparable between the two inventory types, we assigned species in the LFI data to the same species groups that are available in the NFI, i.e. RAS, birches and Scots pine. A note on *Salix*: LFI tallies all *Salix* specimens while NFI only tallies *Salix* specimens with “the potential to grow into trees”. The latter almost exclusively comprises the species sallow (*Salix caprea*), because other *Salix* species in Norway typically are not of tree potential (there may be a few specimens of *Salix pentandra*, *Salix myrsinifolia* and *Salix aurita*). In the LFI data used for this study, we therefore assigned only sallow of the *Salix* species to the merged group RAS.

2.4. Data analyses

There were 25 ± 4.3 NFI plots within a moose range (mean \pm SE), which we reasoned would be too few to provide representative estimates of stem densities and browsing intensities. We therefore explored how many NFI plots from adjacent areas would be needed to stabilize the variance of these parameters. We started with all NFI plots within the boundaries of the moose range and successively included adjacent plots in increments of five in increasing distance to the centre of the range, but never beyond major shifts in topography, geology or forest type. The latter were manually inspected on maps. We plotted the mean and 95% confidence interval of each parameter against sample size (“rarefaction curves”, Fig. S1). The rarefaction curves did not indicate one general sample size for which the parameter values and confidence intervals stabilized against sample size. Instead, this varied between ranges, some more than others. We settled on 40 plots as the most appropriate generalization (see Discussion).

We constructed similar rarefaction curves for the LFI data as an informal verification of whether their sample sizes were large enough to cover the variations in stem density and browsing intensity present on the moose ranges. We then drew samples in increments of 50 random plots from the complete pool of LFI plots on the range, repeated this procedure 100 times and plotted the parameter values (mean of the 100 repetitions) against the numbers of plots included (Fig. S2). Both stem density and browsing intensity (mean and CI) had clearly stabilized well before our maximum sample size for all ranges except for one where stabilization was less evident (Salsbruket). Based on the plots, we interpreted that the LFI data were an area-representative sample of the moose ranges, which was also expected, given that the plot transects in most cases had been systematically distributed or stratified across ranges. Between 300 and 400 plots appeared to be sufficient for the variables to stabilize and consistently so across the moose ranges. Detailed location maps of the LFI and NFI plots for each range are given in the supplement (Fig. S3).

We analysed the data by using the open-source software, R, version 3.5.1 (R Core Team, 2018). Prior to choosing model structures and specificities of tests, we explored the data distribution by using histograms and QQ plots. After testing, we also inspected the fits of all models by looking for patterns in the QQ plots of residuals (Zuur et al., 2007). We tested data partly at the plot level (with input data as measured in the plot) and partly at the range level (with input data being the means across all plots within the moose range). At the range level, most variables did not strongly follow a normal distribution, which was mainly due to small sample sizes, especially for the NFI data.

We explored the influence of data transformations for all range-level models, but none completely removed the slight patterns seen in the residual plots. In our final analyses, we therefore used non-transformed data. Originally, we ran plot-level analyses with ranges nested in regions as a random intercept effect (‘lme’ in R). However, because all random effects were negligible (high residual: variance ratio), we repeated the analyses with non-nested models (‘lm’ in R), with and without the interaction terms of range*inventory type. We omitted the Gjøvik range from any analysis involving browsable biomass or browsing intensity of pine, since pine was not present in the data from this range. We did include the Gjøvik range in the density comparisons between the NFI and LFI, however, since both inventories should reflect the scarcity of pine within this range.

Using the LFI data, we first calculated the species-specific proportions of stems in the height segment 30–130 cm of all stems within the browsing height of moose (30–300 cm). We similarly calculated species-specific proportions with regard to the browsable biomass produced by these stems. We did this by first computing the plot-specific biomass per stem of the species (hereafter abbreviated as shoot-m/stem), which we defined as its plot-representative CAG length per unbrowsed shoot (measured here in metres) * number of unbrowsed shoots per stem. Thereafter, we multiplied the shoot-m/stem by the species’ stem density in the plot to obtain its plot-specific biomass per unit area (hereafter abbreviated as shoot-m/ha). We performed these calculations for each of the two height segments (e.g., 30–130 cm and 30–300 cm). We tested whether the biomass *per stem* showed a linear relationship to stem density at the range- and regional levels (using ‘lm’ in R). Finally, from the LFI data only, we tested whether the biomass *per unit area* (shoot-m/ha) showed an isometric relationship (1:1) to stem density at the range- and regional levels (using ‘lm’ in R). To obtain similar units for the two variables, we centred (observations minus means of all observations) and scaled (divided by the mean) the data. We used the mean as the reference scale to directly interpret the coefficients of slopes relative to a 1:1 relationship.

We subsequently tested species-specific relationships between the LFI and NFI regarding stem density. We first used linear models (‘lm’ in R) on plot level data with stem density as the response variable and inventory type plus range as predictors to test whether one inventory type significantly over- or underestimated density relative to the other inventory. We thereafter used the slope coefficients from the linear regressions with data from the range level to evaluate whether the relationship between the two inventory types was isometric.

Finally, we tested the species-specific relationships between the LFI and NFI estimates of browsing intensity (% of shoots browsed in winter). We tested these proportional data using ‘lm’ in R. An alternative would be to use a logistic model. However, we did not have the underlying binary count data of browsed versus unbrowsed shoots from the NFI which is required in a logistic model. For RAS, all data fell within the middle range (30–70%). There were some observations at the lower end of the scale for pine (down to 10%) which may possibly cause unrealistic predicted values from a linear model, i.e. below 0% (Long, 1997). This was not a concern in our study as we did not use predicted values, but only the regression slope coefficients. We used these to evaluate whether the relationships of browsing intensity between the two inventory types were isometric at the range level. The 10th NFI cycle (years 2010–2014), which was generally used in this study, recorded browsing intensity as the proportion of shoots browsed during the last winter (from year $t-1$ to t where t is the year of inventory). However, the browsing intensity index in the LFI data used in this study also included browsing from previous winters (i.e. browsing accumulated over several winters), as did the NFI previously in the 9th cycle, 2005–2009. We therefore used the NFI data from the 9th cycle for these analyses. NFI browsing intensity data were only recorded for RAS and pine in the 9th cycle, so we could not compare the relationships for birch.

3. Results

3.1. Is stem density a good indicator of food biomass for deer?

According to the LFI, the stems with heights of 30–130 cm comprised $87 \pm 14\%$ (RAS), $57 \pm 3.6\%$ (birch) and $65 \pm 4.4\%$ (pine) (mean \pm SE across ranges) of the total species-specific stem density within the browsing reach of moose (30–300 cm). These stems contributed $88 \pm 2.9\%$ (RAS), $56 \pm 2.9\%$ (birch) and $69 \pm 3.4\%$ (pine) of the species-specific browsable biomass within the reach of moose (mean \pm SE). Stem proportions differed between regions: WEST had more of its total number of browsable pine stems in the 30–130 cm height segment ($t_{14} = 2.3$, $p = 0.038$), and tended to have fewer of its RAS stems in the 30–130 cm height segment ($t_{15} = -2.0$, $p = 0.067$), than other regions. For pine, the regions also differed significantly in their proportions of browsable biomass in the 30–130 cm height segment: WEST, INNL and especially TRON ($t_{14} = 5.2$, $p \leq 0.001$) had more of their pine biomass on stems at 30–130 cm heights compared to EAST.

The browsable biomass per stem at 30–130 cm heights was 37.6 ± 1.4 cm (RAS), 111.3 ± 2.5 cm (birch) and 176.3 ± 10.1 cm (pine) (mean \pm SE across ranges). The biomass per stem differed strongly between ranges (RAS $F_{15,3156} = 10.0$, $p \leq 0.001$, birch $F_{15,1934} = 11.6$, $p \leq 0.001$ and pine $F_{14,995} = 1.9$, $p = 0.021$) and between regions (RAS $F_{3,3168} = 8.0$, $p \leq 0.001$, birch $F_{3,1946} = 15.7$, $p \leq 0.001$ and pine $F_{3,1007} = 3.0$, $p = 0.029$) (Fig. 2). Nonetheless, the stem density and browsable biomass density (shoot-m/ha) were positively related (RAS $t_{15} = 4.1$, $p \leq 0.001$, birch $t_{15} = 3.4$, $p = 0.006$, pine $t_{14} = 6.1$, $p \leq 0.001$, centred and scaled data) (Fig. 3a-c). This means that for all three plant groups, the browsable biomass increased with a slope that was not significantly different from 1. The stem density in the height segment 30–130 cm was therefore an isometric index of the species-specific browsable biomass in this height segment across moose ranges. The coefficient of determination was higher for RAS ($R^2 = 0.54$) and pine ($R^2 = 0.74$) than for birch ($R^2 = 0.45$).

3.2. Relationship between NFI and LFI for stem densities

Stem density did not differ between inventory types at the range level (Table 2). There was a significantly positive relationship between stem densities in the NFI and LFI across ranges for all plant groups (RAS $R^2 = 0.50$, $t_{15} = 3.7$, $p = 0.022$, birch $R^2 = 0.53$, $t_{15} = 4.0$, $p = 0.001$, pine $R^2 = 0.44$, $t_{15} = 3.3$, $p = 0.005$). The slope was close to 1 for RAS (mean $\beta = 1.1 \pm$ SE 0.29) and pine ($\beta = 1.1 \pm 0.34$) with an apparent decreasing model fit (larger residuals) at higher densities (Fig. 4a, c). For birch, the slope deviated more from 1 ($\beta = 0.6 \pm 0.15$), and the NFI tended to be higher than LFI for ranges with low stem densities, but lower than LFI for ranges with high stem densities.

3.3. Relationship between NFI and LFI for browsing intensity

There was a significant interaction between inventory type and range for the mean accumulated browsing intensity (% of shoots browsed in winters) (Table 2). For RAS, there were two ranges which contributed to this interaction: Finnskogen ($t_{15} = -3.6$, $p \leq 0.001$) and Kjøse ($t_{15} = -3.3$, $p \leq 0.001$). The NFI showed lower values than the LFI for both these ranges. For pine, the NFI showed generally higher browsing intensities than the LFI except for the Salsbruket range ($t_{14} = -2.6$, $p = 0.009$). The relationship between the two inventory types was nevertheless significant across ranges for pine (mean $\beta = 0.74 \pm$ SE 0.30, $t_{14} = 2.5$, $p = 0.028$), but not for RAS ($\beta = 0.61 \pm 0.47$, $t_{15} = 1.3$, $p = 0.218$) (Fig. 5a, b). The relationship for RAS was significant if we removed the Finnskogen and Kjøse ranges as outliers ($\beta = 1.00 \pm 0.44$, $t_{15} = 2.3$, $p = 0.044$) although much of the variation remained unexplained. For pine, there was a similarly

strong effect by removing the Salsbruket and Aurskog S ranges as outliers ($\beta = 0.95 \pm 0.22$, $t_{14} = 4.3$, $p \leq 0.001$).

4. Discussion

In this study, we investigated the relationships between two types of field inventories concerning estimates of browse availability and browsing intensity for forest deer: one inventory was spatially extensive but with low resolution (National Forest Inventory, NFI), and one inventory was spatially limited but with high resolution (local inventories of moose ranges, LFI). Our main goal was to evaluate whether the crude NFI data on deer browse reflected similar patterns as the detailed data in the LFI. We found that, according to LFI, 1) stem densities in the NFI may be a useful but low-resolution index of species-specific availability of at least two of the three most important browse species groups for deer in Scandinavia and 2) the relationship between the NFI and LFI regarding browsing intensities was generally weak, but still significant for pine. It is likely beneficial to adjust both inventory types for how browsing intensities are estimated, for which we provide specific advice below.

4.1. Is stem density a good indicator of food biomass for deer?

The main question addressed in this study was: To what extent do the densities of stems with heights of 30–130 cm reflect the total winter browse availability for moose and other deer in boreal forests? Moose are up to about 200 cm tall (Franzmann et al., 1978) and have fairly short necks. They can therefore only reach browse up to 300 cm above ground and occasionally higher (e.g., Bergqvist et al., 2013). However, the nutritional quality of browse varies with plant age and thus with tree height (Wam et al., 2016). All browsers, including moose, select for particular nutritional profiles in the food they ingest (Felton et al., 2016; Wam et al., 2018). This means that trees of different heights present different nutritional values for the animal. Snow conditions also influence which plants and plant parts are available for browsing. Moose, for example, can use pine trees (a winter staple food) that are taller than 150 cm more intensively than they use shorter ones (Borkowska and Konopko, 1994), while they can use rowan trees (a food source used year-round) with lower heights more intensively than they use rowan trees with taller heights (Edenius and Ericsson, 2015). Therefore, in any field survey of browse availability for deer, all stems within the browsing reach of the animal of interest should ideally be included. For moose, these would be those stems with heights of 30–300 cm.

According to the LFI data, there were differences between plant species in terms of the proportions that stems with heights 30–130 cm comprised of all the species-specific browsable biomass available to moose (30–300 cm): RAS had 87% of the biomass in stems with heights 30–130 cm, while birch had 57% and pine had 65% (means across moose ranges). This indicates that a food index based on stems only in the height segment 30–130 cm will underestimate the available biomass of birch and pine relative to RAS at any given moose range. The proportions also differed between ranges. In particular, one range in the WEST with a less intense browsing history than is typical for that region (Revetal, Fig. 5a) had proportionally fewer stems in the height segment 30–130 cm: 46% for RAS, while the mean for WEST was 75%. Growing conditions are fairly similar for RAS on all the ranges in WEST region. It is therefore likely that the greater heights of RAS on the Revetal range were due to the lower browsing intensity. Other studies have found that intense browsing affects the duration that trees stay within height segments (e.g., Edenius and Ericsson, 2015). Browsing intensity over time thus shapes the height distribution of these trees. This adds uncertainty to how well the stem densities in a given height segment reflect the total browse available to deer at all browsing heights.

For stem density alone to be a useful indicator of food availability for deer, it must also correlate well with the browsable biomass on

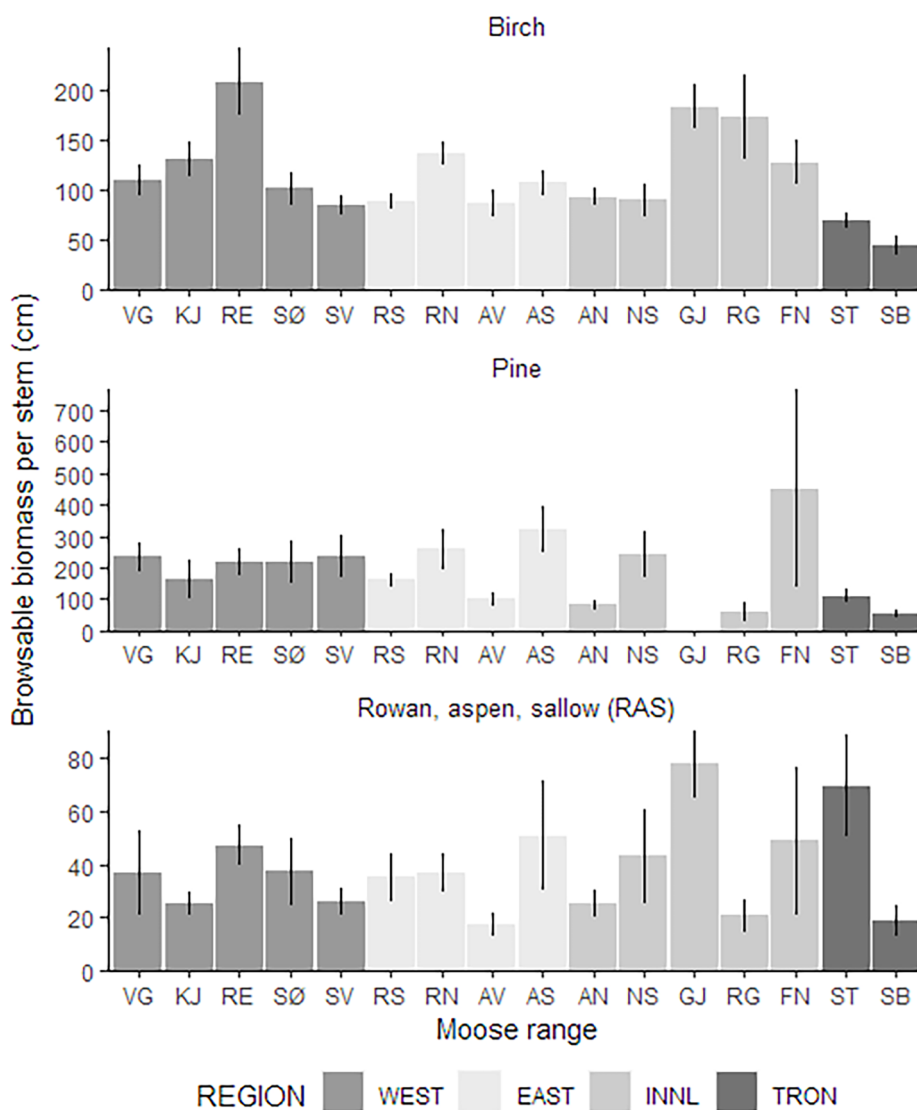


Fig. 2. Amount of browsable biomass per stem (tree height 30–130 cm) (mean ± SE) in terms of the summed lengths of all unbrowsed shoots of current annual growth, as measured on sample trees considered to be representative of plant growth vigour and deer browsing intensity for the study plot (plot size 12.5 m²). Data are from local field inventories (LFI) on 16 moose ranges in southern Norway, 2005–2016. Total sample sizes (sums across ranges) = 3172 RAS stems, 1950 birch stems and 1012 pine stems which were sampled in plots distributed across the entire forested area of the moose range.

those stems and equally so for all stem height segments of interest. The amounts of browsable biomass per stem generally vary among plant species (e.g., Nordengren et al., 2003; Konôpka and Pajtk, 2015) and between areas, e.g., being higher with more fertile growing conditions and lower with higher browsing intensities (Wam et al., 2010). In our study, the mean browsable biomass per stem (30–130 cm) varied strongly across ranges (Fig. 2). Combined with the ranges’ varying proportions of browsable stems in the 30–130 cm height segment, the relationships between stem density and browsable biomass in our study must be considered to be highly site-dependent. Nonetheless, the browsable biomass per ha (on 30–130 cm tall trees) showed a positive isometric relationship (1:1) with stem density across ranges and closely so for pine and RAS. This is because stem density had stronger leverage than biomass per stem due to its higher variation across ranges. The difference between the highest and lowest values of the ranges’ mean stem density was 125 times (RAS), 1770 times (birch) and 460 times (pine) higher than it was for the ranges’ mean biomass per stem. We found a less isometric relationship for birch compared to pine and RAS which may be explained by regional differences in the growth vigour of birch. Birch produces substantially more shoot biomass per stem on

more fertile soils and the influence of soil fertility is much stronger for birch than for pine and RAS (Wam et al., 2010).

Although the relationships of stem densities and biomass per ha were sufficiently close to being isometric for trees with heights of 30–130 cm, caution should be exercised when using only this tree height segment to evaluate browse availability for moose. The proportion of all trees within moose browsing reach (30–300 cm) that were in the 30–130 cm tree height segment differed among plant species. According to our study, areas with more birch and pine relative to RAS are likely to have more browsable biomass than is indicated by an index based on the 30–130 cm height segment. Likewise, areas with more RAS relative to birch and pine are likely to have less browsable biomass than is indicated by this index. The density-dependent biomass per birch stem adds to the uncertainty of available birch browse. The higher the share of RAS among all stems of the three species groups, the 30–130 cm stem index more closely reflects the number of all stems within moose browsing reach. RAS had more of their stems below 130 cm, because they are the plants that are most selected by moose (Wam and Hjeljord, 2010) and are generally growth-stunted in southern Norway unless physically protected from browsing, e.g.,

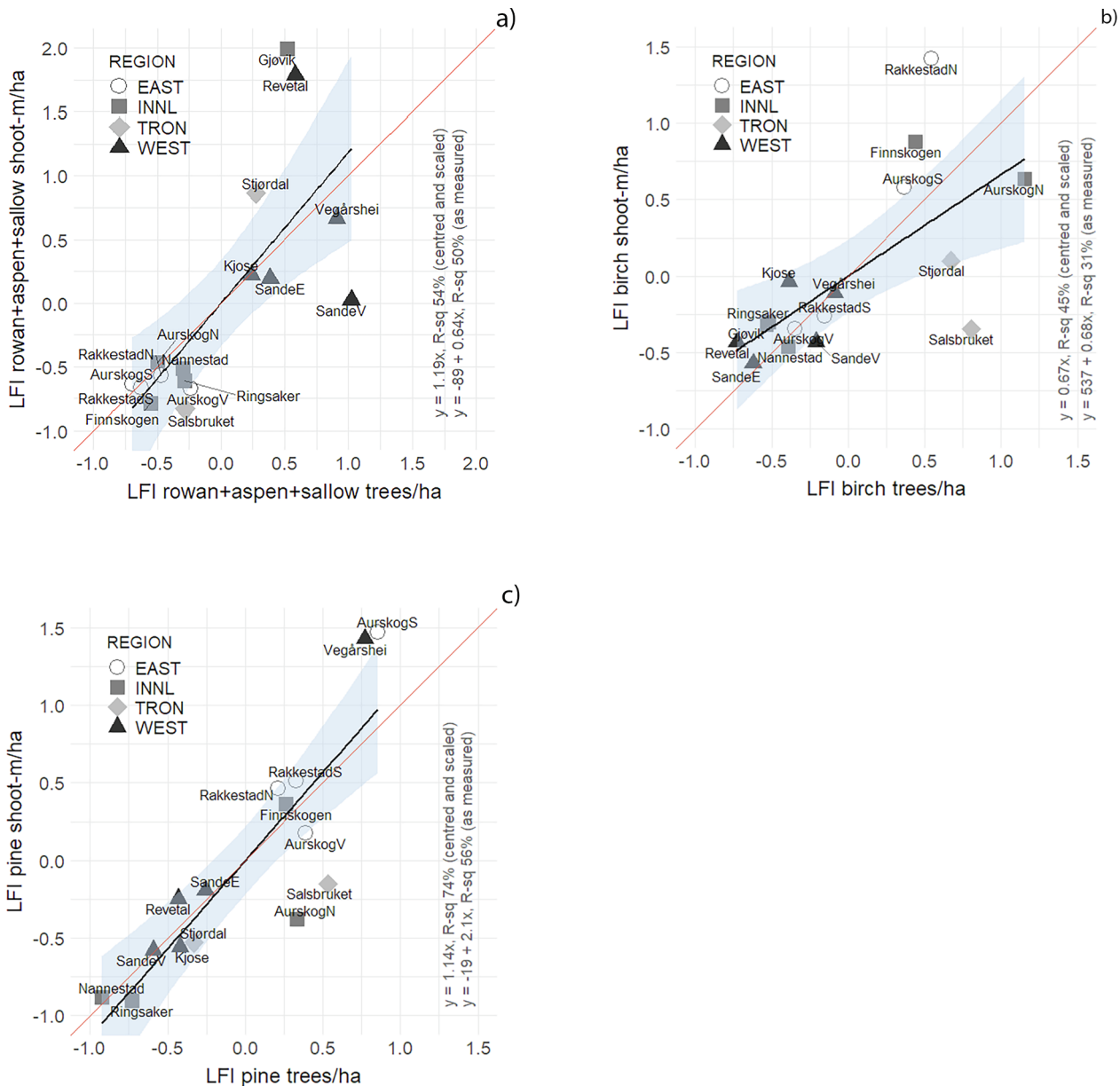


Fig. 3. a-c. Relationships between stem densities in the tree height segment 30–130 cm and mean browsable biomass (summed lengths of the current annual growth (CAG) of shoots) on 16 moose ranges in four forest regions of southern Norway. Data are from local field inventories (LFI), 2005–2016. Shaded areas are the 95% confidence intervals of the regression slopes (black lines). Regression equations are given at the far right of the figure. CAG was measured on 3172 RAS stems, 1950 birch stems and 1012 pine stems (total across all ranges). Mean values were centred and scaled to show the slopes relative to a hypothetical isometric (1:1) relationship (red lines). Regression equations based on the original data are also given as a reference for future studies.

exclosures (Speed et al., 2013).

4.2. Coherence between the NFI and LFI regarding stem densities

The relationships between the NFI and LFI for stem densities (of heights 30–130 cm) were generally strong, but for several moose ranges it was necessary to include NFI plots from neighbouring areas to obtain sufficiently high sample sizes. Four ranges had < 15 NFI plots within the boundaries of the range, with nine being the minimum. The rarefaction curves did not indicate one general sample size for which the parameter values and confidence intervals stabilized against sample size (Fig. S1). Instead, this varied between ranges. We chose 40 NFI plots to be the most appropriate generalization. Using more than 40 plots in some cases destabilized the values, which we consider to be an effect of including NFI plots that were more distant from the moose

range surveyed by the LFI. These NFI plots were likely to be from areas that were ecologically different from the moose ranges. In small areas, especially with high spatial variations, the NFI plots may be too few to adequately capture the variations in deer browse.

We believe that for some purposes, stem densities can still be an adequate index of relative browsable biomass availability across areas, especially if the whole browsing height of the animal of interest (30–300 cm for moose) is included. For example, stem density should be useful for comparing large-scale differences in browse availability at the national level (e.g., Hörnberg, 2001). Additionally, stem densities can be used to roughly identify whether relative changes in food availability occur over time within a given area. If such changes include major shifts in plant species compositions, however, changes in stem density may not adequately reflect changes in browsable biomass, because plant species have different biomass per stem. What is adequate

Table 2

Number of study plots, density of browsable trees of height 30–130 cm (stems/ha) and proportion of shoots browsed in winter at 16 moose ranges in southern Norway (mean \pm SE across ranges) as estimated by two types of inventories: NFI = the National Forest Inventory (plot density 0.3 km⁻²) and LFI = local inventories of moose browsing (plot density 2–3 km⁻²). Linear regression models were run with data at the plot level. For stem densities, all plots were included regardless of the presence of a given plant species. For browsing intensity, only plots with a presence of the plant species were included. Plot sample sizes for browsing were therefore lower for browsing intensity than for stem density¹. The overall degrees of freedom for the *F*-statistics were similar for all factors, but are shown only for 'Range'. n.s. = not significant.

Response variable and plant group	NFI	LFI	Linear regression statistics		
			Inventory type	Range	Inventory*Range
Stem density					
RAS	40 \pm 3 plots	641 \pm 59 plots			
Birch	1151 \pm 218	1063 \pm 150	n.s.	$F_{15,10887} = 32.8, p \leq 0.001$	n.s.
Pine	834 \pm 110	1004 \pm 144	n.s.	$F_{15,10887} = 16.5, p \leq 0.001$	n.s.
	269 \pm 53	225 \pm 36	n.s.	$F_{15,10887} = 12.9, p \leq 0.001$	n.s.
Browsing intensity					
RAS	24 \pm 2 plots	197 \pm 25 plots			
Pine	48% \pm 1.8	49% \pm 0.6	$F = 0.15, p = 0.697$	$F_{31,3500} = 14.6, p \leq 0.001$	$F = 4.2, p \leq 0.001$
	28% \pm 2.1	19% \pm 0.9	$F = 20.9, p \leq 0.001$	$F_{31,1201} = 13.5, p \leq 0.001$	$F = 2.4, p = 0.002$

¹ The mean numbers of plots per range are shown for RAS in the table. For pine, the number of plots is lower: NFI = 15 \pm 1 plots and LFI = 67 \pm 10 plots.

depends on the level of detail for which the data will be used. Stem densities can also be useful in preliminary studies before conducting more detailed investigations or for examining species-specific patterns when the presence of other species is not of particular interest. For example, [Pettersson et al. \(2019\)](#) successfully used Swedish NFI data to study temporal variations in the recruitment of oak *Quercus* spp. subjected to changing browsing pressures from varying deer densities.

4.3. Discrepancies between the NFI and LFI regarding browsing intensity

The relationships between the NFI and LFI in their browsing intensities were weak (R^2 11% for RAS and 32% for pine), yet significant for pine. We can see three possible explanations for the lack of stronger relationships: (1) the two data sets did not overlap in time, (2) there were systematic differences between the NFI and LFI for how browsing intensity was estimated in the field, or (3) there was uncertainty in the estimates which was caused by difficulties in identifying browsed and unbrowsed shoots. It is also worth repeating that the sample sizes per range were small for the estimates of browsing intensities, especially in the NFI data. The effect of removing outliers in our browsing intensity data was substantial.

Regarding the first explanation (i.e. inventories not overlapping in time), the LFI data came from 2005 to 2016 while the NFI data on browsing came from 2005 to 2009. There is no doubt that browsing intensities vary between years due to changes in animal densities or extreme variations in weather conditions. For example, both high-snow years and dry summers may contribute to higher browsing intensities ([Wam and Bless, 2018](#)). However, in this study we used an index of browsing that had accumulated over several winters, which should be less affected by weather variations. Over multiple years, the influence of isolated years with non-normal weather conditions diminishes. Furthermore, since the NFI consistently showed a higher pine browsing intensity than the LFI, we believe that the discrepancy cannot be explained by temporal weather changes or animal densities.

A more likely explanation is that there are systematic differences in how the browsing intensity is estimated in the two surveys. The NFI and LFI did not collect the browsing intensity data used in our study in exactly the same way. In the NFI, the browsing index is estimated as the number of shoots browsed divided by the sum of browsed and unbrowsed shoots with growth from last year. In the LFI, browsing intensity is calculated as the number of shoots browsed divided by the sum of browsed shoots and shoots with growth from the current year (CAG). This by itself should not cause systematic bias, since browsed shoots rarely grow CAG from non-axillary buds ("sleeping" buds on old wood) ([Crawley, 1983](#)). Without shoots from sleeping buds, the number of unbrowsed shoots with old growth equals the number of shoots with the current year's growth. However, this may still be influential, as the

NFI and LFI collect data at different times of the year. In the NFI, the inventories are distributed over the entire growing season, while for the LFI data are collected at the peak of the growing season. Increased branching and leafing may impact the observability of winter-browsed shoots throughout the growing season ([Viken, 2017](#)). This can lead to systematic bias, or at least variability, between the NFI and LFI regarding the extent to which browsed shoots are identified. Field experiments would be needed to identify the nature of this possible bias. We believe that it is generally easier to correctly identify unbrowsed shoots if the CAG shoots are examined (as the LFI does) instead of shoots from the previous year's growth (as the NFI does). The base of CAG under most conditions retains a different colour and texture than last year's growth until at least the peak of the growing season (H.K. Wam, personal observation), while after the peak of the growing season, it becomes increasingly difficult to separate last year's growth from older growth. A disadvantage of using CAG is that the inventory cannot begin before the shoots have started elongating in the spring.

Both the NFI and LFI undoubtedly have uncertainties in their data on browsing intensities. Counting shoots and distinguishing deer browsing from other damage is inevitably difficult under certain circumstances, especially for highly branching plant species. Birch growing on shaded and less fertile soils, for example, is more likely to invest in 'short shoots' than 'long shoots' ([Maillette, 1982](#)) and therefore has miniscule lengths of their typical CAG. Separating deer browsing from damage caused by drought, insects or mechanical forces is inherently subjective and imprecise (H. K. Wam, personal observation). This may explain the greater discrepancies between the NFI and LFI regarding browsing intensities for birch than for pine.

There is value in knowing not only the browsing intensity from last winter but also the browsing that has accumulated over previous winters. Moose populations may be heavily culled between NFI cycles. If the browsable plants were severely damaged by moose browsing prior to the cull, neither last winter's browsing nor the stem density alone tell a realistic story. In such a scenario, there will be many stems, but each can produce only a small amount of browsable biomass ([Danell et al., 1994](#)). At the same time, last winter's browsing will be low, and if only these data are examined, one cannot detect that the production of biomass on the stems is below normal. The separation of last winter browsing and previous winter browsing was implemented in the LFI protocol in 2018 as a result of this study and should preferably also be included in the NFI. Prior to 2018, all winter browsing was grouped in the LFI, regardless of the year in which it occurred. Recording browsing into different classes of occurrence times can provide forest managers with valuable information. If a forest stand has been browsed intensively over years, its recruited trees are likely to be more damaged than if they had only recently been browsed ([Chouinard and Filion, 2001](#); [Čermák et al., 2009](#)). In the Finnish NFI, browsing ages have been

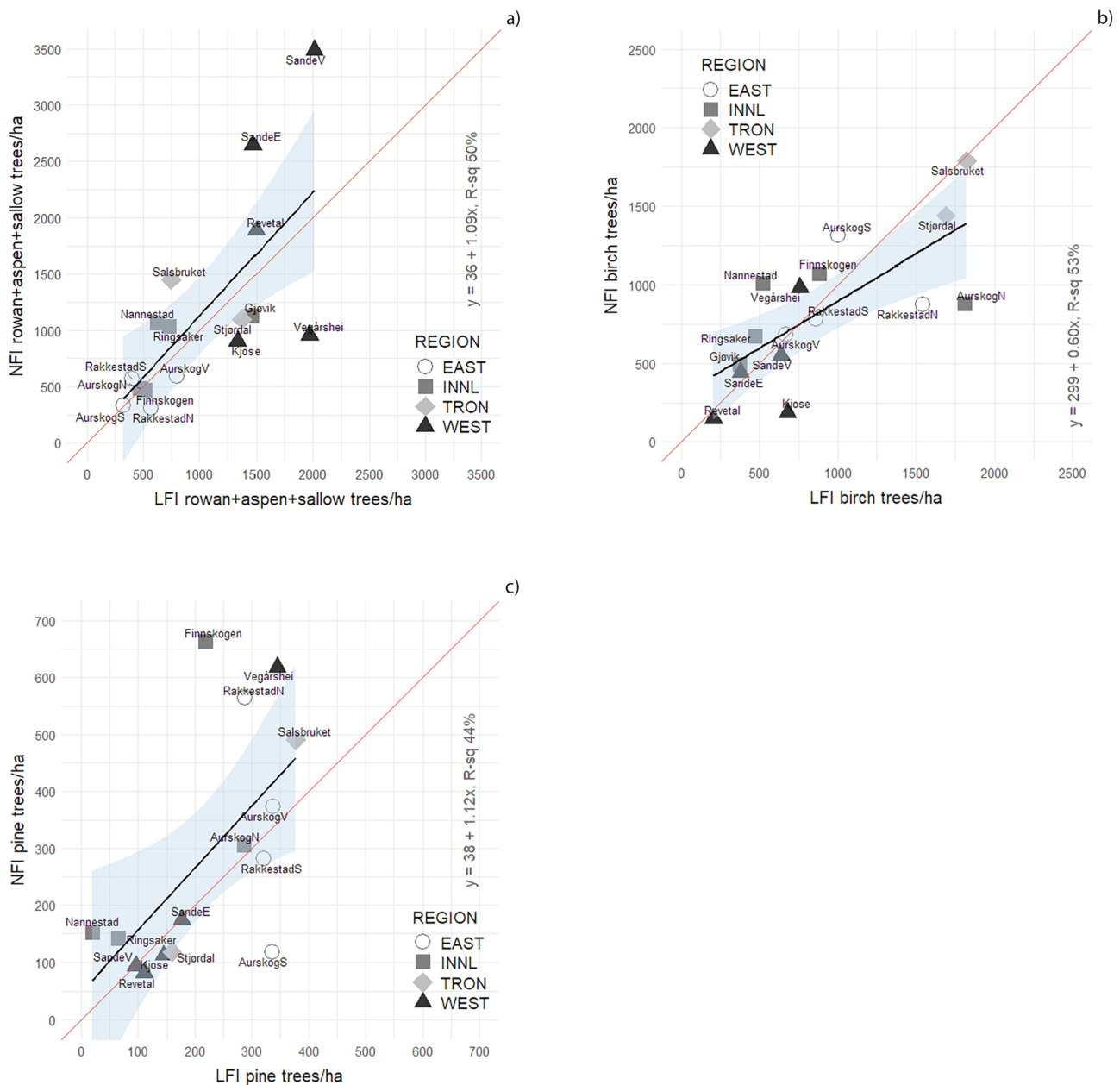


Fig. 4. a-c. Relationships between the two different inventory types regarding their mean tree densities (height 30–130 cm) across 16 moose ranges in four forested regions of southern Norway. NFI = National Forest Inventory of Norway, data are from $N = 40 \pm 3$ plots (mean \pm SE) per range sampled in 2010–2014. LFI = local field inventories of moose browsing, data are from $N = 641 \pm 59$ plots per range sampled in 2005–2016. Red lines indicate hypothetical isometric (1:1) relationships. Shaded areas are the 95% confidence intervals of the regression slopes of (black lines). Regression equations are given at the far right of the figure.

separated into five classes (Nevalainen et al., 2016). Forest stands that are in the most need of restorative silvicultural actions can thus be identified. If the browsing index is split, however, it is important to ensure that the existing data are comparable with future data to conserve their value as time series (see the informative illustrations in Kupferschmid et al., 2019).

National forest inventories are carried out in nearly all European countries (Tomter, 2016) and are regularly used to monitor deer browsing (see references elsewhere in our discussion). Recently, such large-scale inventories have also been implemented in North America (e.g., Patton et al., 2018), where browsing indices are needed due to overabundant deer. This means that we now have fairly similar and ongoing, regular inventory schemes for temperate-boreal forests and deer browsing across much of the Northern Hemisphere. To the greater extent that these indices are made comparable across countries, the

more global value the data will have. It can therefore be highly valuable to conduct more studies on how the methodological aspects influence the outcome and usefulness of the indices.

5. Conclusion

Using stem densities in national forest inventories (NFI) can be an efficient but low-resolution way to monitor browse availability for deer, provided that the full range of stem heights reachable for the deer of interest is included (e.g., 30–300 cm for moose). Trees should preferentially be tallied into at least 2–3 height classes so that relevant data can be easily extracted for other animal species as well. All major browse species should be included, because their availability relative to each other affects the accuracy of stem density as an index of the available browsable biomass. It is also a prerequisite that the number of

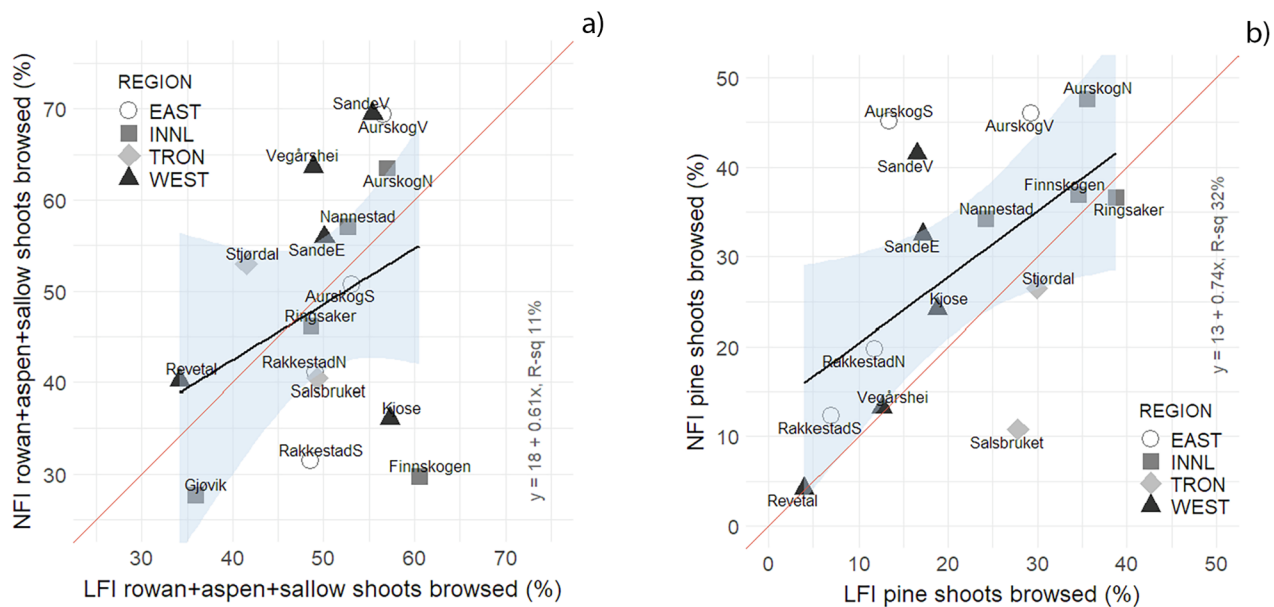


Fig. 5. a-b. Relationships between two different inventory types regarding their mean estimated proportions of winter-browsed shoots on stems with heights of 30–130 cm across 16 moose ranges in four forested regions of southern Norway. NFI = National Forest Inventory of Norway, data are from 2005 to 2009. LFI = local field inventories of moose browsing, data from 2005 to 2016. Number of plots (=sample sizes) = 24 ± 2 RAS and 15 ± 1 pine (NFI), or 197 ± 25 RAS and 67 ± 10 pine (LFI) per range (mean \pm SE). Red lines indicate hypothetical isometric (1:1) relationships. Shaded areas are the 95% confidence intervals of the regression slopes of (black lines). Regression equations are given at the far right of the figure.

NFI plots is large enough to cover the spatial variability of the area being studied. To make any index of browsing intensities more useful, we suggest to separately record the browsing from last winter and the browsing from previous winters. Ideally, browsing should be recorded in terms of the numbers of shoots (browsed and unbrowsed), instead of as proportions, as the former approach gives more options for later calculating various versions of the browsing indices.

Data statement

The data that support the findings of this study can be obtained from the corresponding author upon request.

CRediT authorship contribution statement

Hilde Karine Wam: Conceptualization, Methodology, Investigation, Resources, Data curation, Formal analysis, Validation, Writing - original draft. **Erling Johan Solberg:** Conceptualization, Methodology, Data curation, Formal analysis, Validation, Writing - review & editing. **Rune Eriksen:** Resources, Data curation, Validation, Writing - review & editing. **Aksel Granhus:** Funding acquisition, Writing - review & 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106967>.

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