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## A guide for selecting the appropriate plot design to measure ungulate browsing



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#### ABSTRACT

Ungulate browsing often impairs tree regeneration, thus preventing the achievement of economic or conservation goals. Forest ungulate management would thus benefit from a practical decision tool that facilitates method selection from a wide range of monitoring methods and indicators currently available. In this study, we first provide an overview of the different browsing-impact monitoring methods and indicators currently applied. We then present a newly developed decision matrix for method evaluation that can assist forest stakeholders in choosing the browsing-impact monitoring method best suited to their needs, based on the selected indicators. The first step involved two separate literature reviews to create an overview of the currently applied methods and to select the indicators best suited for measuring browsing impact. Three types of indicator groups with their respective parameters were considered important for method evaluation: browsing indicators (e.g. regeneration density, browsing incidents), performance indicators (e.g. expense, expertise) and data quality indicators (e.g. susceptibility to measurement errors). Subsequently, all parameters defined within each indicator group were categorised and a grade was assigned to each category. To create the final method-indicator matrix, each browsing-impact monitoring method received a grade for each parameter within all indicator groups, reflecting the specific advantages and disadvantages of implementing the respective parameter within a specific method. The utility of the matrix in selecting the most suitable monitoring method was then demonstrated using the example of Germany's national parks. Based on the weights added to the method-indicator matrix, as defined by national park representatives, and considering local requirements the nearest-tree method was favoured over the other two methods. This newly developed matrix provides a more scientific objectification of ungulate browsing-impact measures and can be easily used by forest managers to address their own requirements, based on a consideration of the advantages and disadvantages of the included methods.

#### 1. Introduction

Ungulates are recognised as ecosystem engineers, as they strongly influence the structure, composition and development of terrestrial ecosystems (Gill, 1992; Smit and Putman, 2010). However, the increased density of ungulate populations across many temperate regions (Apollonio et al., 2010) has intensified the effects on forest ecosystems to an extent that has provoked intense discussions among foresters, wildlife managers and scientists (Côté et al., 2004; Valente et al., 2020). Browsing

by ungulates adversely impacts forest regeneration density (Tremblay et al., 2007; Kuijper et al., 2010) and tree diversity (Gill and Beardall, 2001; Rooney and Waller, 2003; Schulze et al., 2014), which, among other consequences, may limit the ecological resilience of the affected forest to climate change (Morin et al., 2018). Nonetheless, any consideration of the successional dynamics of forests must take into account the differential responses of trees to browsing, which depends on the traits of the affected species, the site conditions and the impact history (Gill, 1992; Edenius et al., 1995; Cailleret et al., 2014; Kupferschmid et al.,

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2017). Indeed, rather than a decrease, some studies have found a neutral (Pellerin et al., 2010) or even an enhancing (Boulanger et al., 2018; Simončič et al., 2019) effect of browsing on biodiversity as well as the overcompensation of tree growth under certain conditions (Kupferschmid and Bugmann, 2013). These contradictory findings partly explain the differing opinions on the appropriate management of ungulate browsing in forest ecosystems (Reimoser and Putman, 2011) and the ongoing discussions on the optimal approaches to measure and understand browsing effects in the field (Reimoser et al., 2014; Huber et al., 2018).

Regardless of the management focus or whether the effects of ungulate browsing are interpreted as positive or negative, managers need accurate information about ungulates and their impact to implement ungulate management policies (Nichols and Williams, 2006). Continuous tree regeneration monitoring is pivotal for assessing browsing trends, as it facilitates open and informed debate about management practices and the trade-offs involved and is thus crucial for adaptive wildlife management. An accurate assessment of the effects of browsing and the subsequent selection of the optimal monitoring method require the formulation of management objectives that serve as clear decision criteria. Informed decision-making relies upon the selection of indicators of browsing effects that are concise, relevant and meaningful to managers, as mistakes in indicator selection can result in an inability to assess policy performance and therefore in unwanted financial or socio-economic consequences (Failing and Gregory, 2003). A prerequisite of indicator selection, and thus in the selection of the most appropriate monitoring method, is a clear understanding of how and to what extent each indicator informs management decision-making (Legg and Nagy, 2006; Lindenmayer and Likens, 2010).

Various methods differing in their measured indicators have been applied to assess the impact of browsing. Although ungulates often target understory vegetation and by regulating tree regeneration, growth, and survival can impact understory plant communities (Gill, 1992; Habeck and Schultz, 2015; Bernes et al., 2018), this study is aimed at facilitating the selection of a scientifically appropriate method by forest managers to measure ungulate browsing impact on the economically valuable tree regeneration layer. We first provide an overview of the wide range of browsing-impact monitoring methods and indicators currently in use. Second, we present a newly developed decision matrix for method evaluation aimed at assisting forest stakeholders in choosing the browsing-impact monitoring method best suited to their needs, based on the selected indicators. This involved the following steps: (i) A literature review was conducted to create an overview of current browsing-impact monitoring methods and (ii) a second literature review to select indicators best suited to measuring browsing impact, and thus to effective monitoring. The method-indicator-matrix was constructed by first assigning grades to each indicator category (iii) to reflect the specific advantages and disadvantages that could be encountered by employing a particular set of indicators. In the second step, a grade for each indicator was assigned to each browsing-impact monitoring method (iv). Last, (v) the utility of the matrix in selecting the most suitable monitoring method(s) was demonstrated in a case study of Germany's national parks.

#### 2. Methods

Browsing-impact methods and ungulate-effect indicators were extracted in two separate literature reviews. The aim was to create a sound summary of the methods used to measure browsing impact on tree regeneration (i) and find useful indicators of browsing effects (ii). A detailed description of both literature reviews is provided in the Supplementary Material.

To evaluate the browsing-impact monitoring methods chosen based on the literature review, the selected indicators were categorised, with a grade assigned to each category (iii). The categorisation was based on a five-point grading system in which 1 or 2 indicated a positive value, and 4 or 5 a negative value. The final method-indicator matrix was then

created by (iv), assigning a grade to each browsing-impact monitoring method for each indicator based on the literature and according to the expert assessments of the authors. The assigned grades reflected the specific advantages and disadvantages of employing the indicator within a specific browsing-impact monitoring method.

Last, when making trade-offs among management objectives, it is crucial to define the relative importance of each indicator (Failing and Gregory, 2003). By altering the weighting of the different indicators, the matrix can be easily adjusted to meet the demands of different stakeholders. The latter can then choose the monitoring method best suited to their needs and therefore obtain objective, sound and comparable data enabling adaptive ungulate management. Within this study, the weights applied as an example reflected the needs of German national park wildlife management authorities as expressed during workshop discussions. For the weighting factors, high importance was indicated by values of 3 or 4 and low importance by values of 1 or 2. An overall grade for each method then calculated follows: Sum (grade parameter×weighting factor for each parameter) Sum (weighting factor for all paramete

#### 3. Results

#### 3.1. Method search

The methods to measure browsing impacts as identified in the literature can be described as fixed-area, fixed-count and *N*-highest tree methods (Table 1).

#### 3.1.1. Fixed-area methods

Fixed-area methods are classical forest inventory approaches with predefined, fixed plot sizes. The number of trees that need to be measured depends on the tree abundance in the plot area (Avery and Burkhart, 2002; Kramer and Akça, 2008). Three types of fixed-area methods are employed: i) methods examining a single plot or cluster of plots, ii) exclosure methods and iii) methods based on expert estimations (Table 1). Both single-plot and cluster-plot methods are also referred to as plot count methods (Huber et al., 2018). The single plot, whether circular or rectangular, is an often-used plot design in forestry (Düggelin et al., 2020). Cluster plots are a group of sub-plots that together form one plot and are distinguished by their spatial arrangement (Kleinn and Vilčko, 2005). They are used to improve data accuracy by allowing for a larger number of measurements per plot, thus reducing the variance (Scott, 1998). In the commonly used exclosure method, measurement results from an open, unfenced plot are compared with those from an adjacent fenced plot in which ungulate browsing is prevented (Abrams and Johnson, 2012). The expert estimation method is a special form of fixed-area plot design in which the attributes of interest are estimated rather than precisely measured (Kennedy and Addison, 1987).

An obvious consideration in selecting a monitoring method is the objective. If this includes density estimations (and estimate precision) or obtaining information of high statistical accuracy on the effect of browsing intensity on stem numbers, a fixed-area method is likely to be appropriate (Cantarello and Newton, 2008). Fixed-area methods offer the statistical advantage of unbiased estimates of tree density, due to their simple geometric relationships (i.e. extrapolation to a larger unit area; Kramer and Akca, 2008). However, this is only the case if the entire plot is measured or an area-based stop criterion is defined (e.g. 1/4 of the plot area). An area-based stop criterion generally reduces the measurement effort, but its pitfalls need to be considered. For example, if the measured sub-area is not representative of the whole plot, the stop criterion can produce over- or underestimations to an unknown degree (Reimoser et al., 2014). This is also true if the stop criterion is based on the number of trees, irrespective of their species (e.g. Rüegg and Nigg, 2003). In that case, there will be a particularly high bias for rare species, depending on whether they are included or excluded by chance. In addition, the plot area will change over time due to tree growth and mortality, thus

**Table 1**Overview of the methods used to assess browsing impact and their advantages/disadvantages.

Method			Short description	Advantages	Disadvantages
Fixed-area methods	Plot-count methods	Single- plot	General: circular, rectangular or quadratic plot shapes (Archaux et al., 2006)     Possibility to include an area-based stop criterion     Objective: ratio of browsed to overall trees	Easily applicable     Statistically accurate in case of no stop criterion     Every tree has the same weight	High measurement effort and potentially high measurement error with high regeneration density     Often relies on small fixed-areas, which compromises the biodiversity estimate     Effort not easily predictable     An area-based stop criterion can be implemented but it may lead to biased results (i.e. density and browsing), in particular for rare species     Ecologically, disproportionate weighting of plots with extensive regeneration (i.e. Quercus in Kupferschmid et al., 2022b)
		Cluster- plot	Similar to the single-plot method, but with several sub-plots  Sub-plots can be placed along a line (transect) (e.g. Gregoire and Valentine, 2007) or according to a point-centred quarter method (e.g. Bryant et al., 2005) or T-square technique (e.g. Krebs, 2014)	See single-plot method     The use of sub-plots increases data precision (reduced between-cluster variance)	See single-plot method     Greater measurement effort than for single-plot and fixed-count methods
	Exclosure		Paired fenced and unfenced control plots     Detection of potential differences between plots (Abrams and Johnson, 2012)	· Shows effects in the absence of ungulates	High maintenance costs     Unknown legacy effects of browsing (Royo et al., 2010)     Absence of ungulates is an artificial, non-ecological state
	Estimation		Attributes are estimated for each plot (Kennedy and Addison, 1987)	· Easily applicable and efficient	Unknown subjectivity per estimation (Cantarello and Newton, 2008); does not provide objective results
Fixed- count methods	N-highest tree	2	<ul> <li>Plot area and number of trees are fixed</li> <li>The highest trees per tree species or species groups are measured (Reimoser et al., 2014)</li> <li>Objective: ratio of browsed trees to highest trees</li> </ul>	Efficient, as a limited number of measurements are needed     Focus on trees that could later become dominant     Results less influenced by dense regeneration plots	Browsing determined only on the most vital trees     Vital trees are more browsing prone, which can lead to biased browsing estimates     Highly biased regeneration density     Biased comparison between species, as they often differ in height
	K-tree		<ul> <li>• <i>K</i>-nearest trees to plot centre are measured (Kleinn and Vilcko, 2006b); where k ≥ 3</li> <li>• Objective: ratio of browsed trees to overall trees</li> <li>• Measurement stop criterion kth tree or max. search distance</li> </ul>	Effort is approx. the same over all plots such that the total effort is easier to predict     Efficient, as a limited number of measurements are needed     Results are less influenced by dense regeneration plots	Biased density estimation due to irregularly distributed trees     Browsing intensity estimator is only less biased when no measurement stop criterion for the search distance is applied
	K-tree cluster		· Like <i>k</i> -tree, but with several sub-plots (e.g. Lynch and Rusydi, 1999)	See <i>k</i> -tree     More sub-plots results in a higher data precision	<ul> <li>See k-tree</li> <li>Greater measurement effort per plot</li> </ul>
	Nearest-tree		<ul> <li>K-nearest trees per species and height class to plot centre are measured (where k = 1 or 2)</li> <li>Objective: stand area stocked with (damaged) trees, i.e. number of grid points with (damaged) trees divided by total number of grid points (Huber et al., 2018)</li> <li>Measurement stop criterion: kth tree or max. search distance (Kupferschmid and Gmür, 2020)</li> </ul>	Bias-free calculation of the occupied area (stocked area) and browsed area  No area measurements needed Results less influenced by dense regeneration plots, as every plot has the same weight (Kupferschmid and Gmür, 2020) Large max. search distances possible and thus the inclusion of rare tree species	<ul> <li>Proportion of browsed trees can be calculated but will be biased due to the max. search distance (similar to k-tree) and the unknown spatial distribution of trees</li> <li>Bias in estimating density measures (similar to k-tree)</li> </ul>

prohibiting later comparisons with older data. Although fixed-area methods with a stop criterion based on a predefined maximum number of trees are very often used in monitoring, they are not further discussed herein due to their high bias. Thus, this study differentiates between single-plot and cluster plots using either no stop criterion or an area-based stop criterion (see Table 1 for details).

#### 3.1.2. Fixed-count method

In fixed-count, or distance-based, sampling methods, the distances between trees and a given point are measured. These methods can be divided into: i) k-tree, ii) k-tree cluster and iii) nearest-tree methods. In the k-tree method, a predefined number of trees irrespective of species (k, where  $k \geq 3$ , but typically up to 20) needs to be measured, with the distance of the k-tree to the central plot point defining the plot size

(Kleinn and Vilčko, 2006a). The k-tree cluster method uses the k-tree approach within a cluster plot design, i.e. a group of sub-plots. For practical reasons, a maximum search distance is defined until the kth tree is searched. The nearest-tree method is based on sampling the tree nearest to the plot centre and is thus a special form of the k-tree method with k < 3. Compared with the k-tree method, the emphasis of the nearest-tree method is on the spatial distribution of the trees (Huber et al., 2018). While in the k-tree method the proportion of browsed trees to overall trees is calculated, in the nearest-tree method the proportion of the stocked area with browsed trees is calculated (Scott, 1998; Huber et al., 2018). Two variations of the nearest-tree method are currently applied as well: i) k-nearest tree measurements independent of tree species (i.e. per height class in the Swiss national inventory; Keller, 2011) and ii) k-nearest trees per tree species and per height class (Kupferschmid

and Gmür, 2020; Angst and Kupferschmid, 2023). The latter method is preferred because information on all tree species locally present are collected and thus various sites can be compared. Consequently, within this study, only the *k*-nearest tree method measured per tree species and tree height class is further considered (referred to in Table 1 as the 'nearest-tree method').

In fixed-count methods, due to the definition of a maximum search distance and the constant workload per species, the measuring effort is generally lower than for fixed-area methods within regions with a relatively low number of tree species (Huber et al., 2018). For managers, the generally reduced working time simplifies both planning and the cost calculation of a browsing inventory (Kleinn and Vilčko, 2006a). In addition, fixed-count methods offer the advantage of covering larger plot

areas and the inclusion of additional plots, thereby increasing the likelihood of including rare tree species (Bryant et al., 2005; Kramer and Akça, 2008; Ramezani et al., 2016). For fixed-area methods, this would be very labour-intensive such that very small fixed plots are often defined, as demonstrated in larger inventories over wildlife sectors (e.g. 0.9 m, Düggelin et al., 2020; or 2 m, Kupferschmid and Gmür, 2020).

#### 3.1.3. N-highest tree method

In the N-highest tree method, the tallest trees per species or species groups are measured within a predefined plot (Reimoser et al., 2014; Rawinski, 2018). Because both the plot area and the number of trees are fixed this method is placed between the fixed-area and fixed-count methods (Table 1).

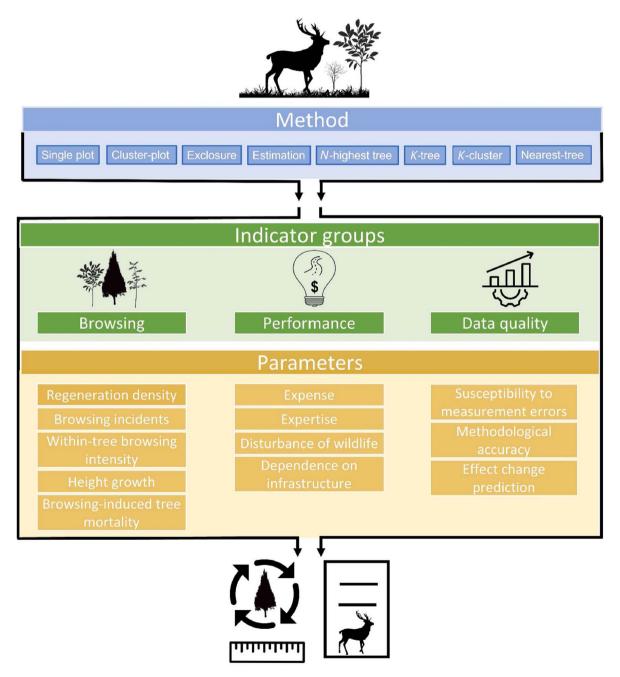


Fig. 1. Overview of the current methods and indicators applied to measure the ungulate browsing impact. Parameters are assigned to three indicator groups: browsing indicators, performance indicators and data quality indicators. To serve as a monitoring tool for adaptive ungulate management, browsing inventories should be conducted regularly.

#### 3.2. Indicator selection

In the second literature research, three types of indicator groups were considered important in the evaluation of browsing-impact monitoring methods: i) browsing indicators, ii) performance indicators and iii) data quality indicators (Fig. 1). For browsing indicators, compositional and functional parameters were included as suggested by Noss (1990). Compositional parameters, such as regeneration density and stocked area, provide information on the spatial arrangement and condition of the tree regeneration, while functional parameters, which describe processes and severity, include browsing incidents, within-tree browsing intensity, height growth and browsing-induced tree mortality. Both types need to be included, because the application of only composition or functional parameters will not allow the detection of a browsing effect or may result in inadequate detection (Kupferschmid et al., 2022a).

Additional parameters evaluating the performance of browsing-impact monitoring methods were added to the matrix, namely expense, expertise, disturbance of wildlife and infrastructure dependence. Because different methods differing in their plot designs will differ in their statistical features, possible constraints were considered in the evaluation of the quality of the output data. Consequently, the following parameters, described as data quality indicators, were included in method evaluation: susceptibility to measurement errors, methodological accuracy and effect change prediction.

#### 3.3. Grading of the selected indicators

To allow the selected parameters for each indicator group to be used as comparison criteria in a method-indicator matrix and thus to identify the most appropriate browsing-impact monitoring method, each of the above-mentioned parameters was graded according to its practicality, efficiency and objectivity. In this section, the categorisation and grading of each parameter are separately discussed for each of the three indicator groups.

#### 3.3.1. Browsing indicators

3.3.1.1. Regeneration density. In studies on forest ecosystems, regeneration density is broadly desired information. Indeed, for some authors, the absolute tree density is a prerequisite for the determination of the extent of browsing incidents (Reimoser et al., 1999). For others, information about the stocked area per tree species is sufficient to evaluate the fulfilment of stocking goals (Stein, 1992; Huber et al., 2018). In the maintenance of biodiversity, it is more important to determine the presence/absence of rare species or neophytes in large plots rather than to accurately calculate the density in very small plots (as rare species or neophytes will mostly be absent). For a statistically accurate determination of tree density, either all trees on a plot or, to reduce the effort, a subset of randomly selected trees on a plot can be counted (Mandallaz, 2006). With the random selection of trees, each subset should be representative of the entire area, such that selection should not be determined based on spatial location or qualitative tree characteristics such as tree height (Table 2). Methods with k-trees independent of tree species generally lead to higher biases in the density approximation per species than is the case with the nearest-tree method, as rare species may not be within the *k*-trees or may be randomly over-represented in the *k*-trees due to a clustered distribution. Categorisation and method grading differentiate among the steps used in density vs. stocked area calculations (Table 2).

3.3.1.2. Browsing incidents and within-tree browsing intensity. Measuring the number or proportion of browsing incidents is an integral step in regeneration monitoring. Attention needs to be paid to the form of the browsed shoots, as it suggests the animal responsible for browsing. For example, a smooth cut surface indicates browsing by hares, whereas

**Table 2**Grading and categorisation of browsing indicator parameters for each browsing-impact monitoring method.

	Categorisation	Methods
Regene	ration density	
1	Tree counting in one plot, bias-free calculation based on a fixed area	Single-plot without stop criterion, single-plot with area-based stop criterion
2	Derivation by distance measurements of <i>k</i> -trees per tree species, with the	Nearest-tree, cluster-plot with and without area-based stop criterion,
	spatial position as the only selection criterion, i.e. bias-free calculation of stocked area per species or derivation by tree counting on several sub-plots	exclosure method
3	Derivation by distance measurements of k-trees independent of tree species, possible bias because of rare tree species	k-tree
4	Derivation by tree distance measurements on several sub-plots or the spatial position of the trees and additional selection criteria	N-highest tree, k-cluster
5 Browei	Estimation by experts ng incidents and within-tree browsing is	Estimation method
1	Measuring effort is independent of regeneration density and thus potentially low	k-tree, nearest-tree, N-highest tree
2	Measuring effort is independent of regeneration density and thus potentially low but may include several sub-plots <i>or</i> a reduced measurement effort by applying a stop criterion	k-cluster, single-plot with area- based stop criterion
3	Measuring effort is potentially high as it is dependent on the regeneration density <i>or</i> because, despite the applied stop-criterion, it includes several sub-plots	Single-plot without stop criterion, cluster-plot with area-based stop criterion
4	Measuring effort is potentially high as it is dependent on the regeneration density and includes several sub-plots	Cluster-plot without stop criterion, exclosure method
5	Individual tree browsing is not measured but instead is only estimated	Estimation method
-	growth	
1	Measuring effort is potentially low as a predefined number of trees are measured	k-tree, nearest-tree
2	Measuring effort is relatively low but is dependent on regeneration density	Single-plot with area-based stop criterion
3	Tree selection results in biased measurements <sup>a</sup> or the measuring effort is increased due to several sub- plots	N-highest tree, cluster-plot with area-based stop criterion
4	Measuring effort is potentially high as it is dependent on the regeneration density, <i>or</i> a subsample has to be defined	Single-plot without stop criterion, exclosure method, $k$ -cluster
5	Individuals are not measured but are only estimated or measuring effort is high as several sub-plots need to be measured	Estimation method, cluster-plot without stop criterion
	ng-induced tree mortality	m.1 .1.1
1	Simple verification because browsing on the reference plot is excluded Regeneration needs to be marked but	Exclosure method
2	k-trees are already chosen by the sampling method	Nearest-tree, k-tree, k-cluster
3	All regeneration needs to be marked.  Measuring effort is dependent on regeneration density but is reduced by an applied stop criterion	Single-plot and cluster-plot with area-based stop criterion
4	All regeneration on sub-plots needs to marked and is dependent on regeneration density or those already selected are biased based on tree characteristic resulting in biased measurements <sup>b</sup>	Single-plot without stop criterion, cluster-plot without stop criterion, <i>N</i> -highest tree
	No measurements on single trees	Estimation method

<sup>a</sup> If only the tallest trees are selected, this results in i) trees of different sizes per tree species such that species cannot be compared with each other and no shift in growth rate ranking can be detected; ii) information on the different size classes of the species is lacking so that the time needed for the trees to grow out of the reach of ungulates cannot be calculated. This can be circumvented by measuring the height increment of k random trees per species.

b By marking the highest trees per plot, mortality estimates are biased in two ways: i) by the lower mortality of taller than of smaller trees (Franklin et al., 1987) and ii) trees of different species within a plot and between plots are not of equal height.

cervids tear off branches, resulting in frayed edges (i.e. Tremblay et al., 2007; Vowles et al., 2016). Incorrect identification of ungulate browsing (i.e. by inclusion of hare browsing or snow damage) can lead to an overestimation of browsing and thus to erroneous conclusions in ungulate management. In addition, understanding long-term ungulate effects on vegetation requires an examination of not only the frequency of browsing but also the strength of browsing of the leading shoot, also referred to as within-tree browsing intensity (Reimoser et al., 2014; Endress et al., 2016; Kupferschmid, 2018). This is crucial, as several studies have shown that ungulates can alter tree height growth responses, with the impact ranging from minimal to a complete suppression of growth (Côté et al., 2004) depending on the amount of tissue removed (Kupferschmid et al., 2015). Within-tree browsing intensity can be characterised, for example, according to whether browsing includes only the terminal buds, large part of the annual terminal shoot or even older terminal shoots (Kupferschmid et al., 2022a). Other possibilities include determinations of leader and lateral shoot browsing (e.g. Kuijper et al., 2013; van Beeck Calkoen et al., 2021). All of the methods described herein can be applied to evaluate browsing incidents and within-tree browsing intensity but they involve different levels of measurement effort that are determined by the number of trees to be measured (Table 2).

3.3.1.3. Height growth. To estimate the impact of ungulate browsing, it is important to know whether browsing causes a shift in the growth rate ranking between species (cf. Krueger et al., 2009). This can be evaluated by measuring the height growth, followed by comparisons of the results between browsed trees and neighbouring trees at both the species and the interspecies level (Kupferschmid and Gmür, 2020; Angst and Kupferschmid, 2023), which may reveal ungulate influence on tree growth in relation to the site conditions (Kupferschmid, 2018). Additionally, based on the height growth per year of trees on a given site and the maximum height of the terminal shoot reachable by ungulates, the period that a tree is vulnerable to browsing can be estimated (e.g. time to reach 1.5 m height; Eiberle and Nigg, 1987; Reimoser et al., 1999). Height growth can theoretically be evaluated with all of the methods discussed herein, which, as already noted, will involve different levels of measurement effort (Table 2). To obtain information on different tree species and different height classes, more trees will have to be measured with the k-tree method than with the nearest-tree. However, as both methods require less measuring effort than other methods, due to the predefined number of trees, they are weighted equally here.

3.3.1.4. Browsing-induced tree mortality. Browsing may not only impair tree growth, it may also inhibit vitality to the extent that the tree dies. However, because the mortality of a tree seedling may have many other causes, involving biotic and abiotic factors, browsing-induced tree mortality should be verifiable. To detect browsing-induced mortality, individual mapping or the marking of selected trees and repeated assessment are crucial (Nomiya et al., 2003). An alternative is to exclude ungulates by fencing and evaluate the differences between the fended and unfenced control plots (Nopp-Mayr et al., 2023). In Table 2, the different browsing-impact monitoring methods are graded according to the measurement effort required for the individual mapping of selected trees.

#### 3.3.2. Performance indicators

3.3.2.1. Expense. The successful implementation of a method depends on efficient work and sufficient financial resources. For long-term monitoring methods, securing finances can be problematic (Legg and Nagy, 2006). However, while expenses should not be reduced to the extent that achieving the desired results is no longer feasible (Mandallaz, 2006), the costs of implementing a method for the desired time should be optimized. Within the grading of performance indicators, mainly material costs were considered, given that personnel costs are difficult to derive because they strongly vary depending on the level of experience and on administrative factors (i.e. contract structure), and the topography and accessibility of the monitoring site considerably influence the effort involved. Assuming that time-consuming methods induce higher personnel costs, estimations of material costs and the time spent on plots were considered in grade assignment (Table 3).

3.3.2.2. Expertise. The expertise needed to apply a method reflects the user-friendliness of that method. Ideally, a method should be easy to understand and implement, but not at the expense of the desired accuracy. Conversely, an overly complex method will discourage managers from its implementation and may incur higher costs (such as if experts are needed) and erroneous data recordings (Andreasen et al., 2001). Thus, for the parameter 'expertise', the grade reflects the knowledge needed to implement the method (Table 3).

3.3.2.3. Disturbance of wildlife. Browsing-impact monitoring may result in the disturbance of wildlife. The manifold effects of human activities on ungulates have been well characterised and include an increase in flight responses (Stankowich, 2008), shifts in day-activity patterns (Bonnot et al., 2020) and changes in habitat selection (Theuerkauf and Rouys, 2008; Proffitt et al., 2009; Pelletier, 2014). Parameter categorisation in this study therefore differentiates between the time needed to conduct the measurements on each plot, depending on the plot design, and whether the method alters a natural, previously undisturbed site (Table 3).

3.3.2.4. Dependence on infrastructure. A method's dependence on infrastructure is a measure of the need for roads or tracks for its implementation. For example, if fences have to be constructed, then roads or in some alpine regions helicopters must be available to transport construction materials and workers, and to control or maintain the constructed structure (Reimoser et al., 2014). If construction or heavy equipment transport is not a prerequisite, the method's dependency on infrastructure is relatively small (Table 3).

#### 3.3.3. Data quality indicators

3.3.3.1. Susceptibility to measurement errors. With an increasing number of measurements in the field, census exhaustion and thus an increased risk of measurement errors may occur, resulting in a higher overlooked rate, duplicative measurements (Avery and Burkhart, 2002; Archaux et al., 2006, 2009) or the erroneous attribution of browsing to ungulates. In addition, the higher the number of measurements required, the greater the likelihood that more personnel will be needed. The differences in expertise can adversely affect the measurements and therefore the results (Archaux et al., 2006; Morrison, 2016). Consequently, susceptibility to measurement errors is categorised based on the measurement effort, i.e. the number of trees measured and the strength of the biases as a result of measurement errors (Table 4).

3.3.3.2. Methodological accuracy. The quality of the output data, i.e. the objectivity and intrinsic biases of data gathered in the field, is a reflection of the methodological accuracy. For example, if a method allows only for subjective data acquisition, neither the accuracy nor the estimation error

**Table 3**Grading and categorisation of performance indicator parameters for each browsing-impact monitoring method.

Grade	Categorisation	Methods
Expense	2	
1	Low-cost, basic equipment (GPS) and only a short time on a plot are needed	Estimation method
2	Relatively low-cost; basic equipment is needed (e.g. GPS device, tape measure, and marking material) and the time on a plot is relatively short	N-highest tree, k-tree, nearest-tree, single-plot with area-based stop criterion
3	Same as 2, but more time must be spent per plot, thus increasing personnel costs	k-cluster, single-plot without a stop criterion, cluster-plot with area- based stop criterion
4	Same as 3, but the increased time spent on several plots increases personnel costs	Cluster-plot without a measurement stop criterion
5	Relatively high (basic equipment and construction material needed)	Exclosure method
Expertis		
1	Can be carried out by unskilled personnel	
2	Can be carried out by personnel with tree-specific knowledge after simple instruction	Single-plot with and without areabased stop criterion
3	Can be carried out by personnel with tree-specific knowledge after instruction regarding plot arrangement or highest tree assessment	Cluster-plot with and without area- based stop criterion, <i>N</i> -highest tree, <i>k</i> -tree, <i>k</i> -cluster, nearest-tree
4	More detailed instruction and/or specific training required	
5	Objective instruction cannot be given, professional knowledge and experience are needed	Estimation method, exclosure method
Disturb	ance of wildlife	
1	Plot visited, but tree regeneration not measured and thus no alteration of the site	Estimation method
2	Measurements once per year, with relatively little time spent on the plot	Single-plot with area-based stop criterion, <i>N</i> -highest tree, <i>k</i> -tree and nearest-tree
3	Measurements once per year, but involving several sub-plots with/ without a stop criterion	Cluster-plot with area-based stop criterion, k-cluster, single-plot without stop criterion
4	Increased measurements on several sub-plots without a stop criterion, or measurements several times per year	Cluster-plot without a stop criterion
5	Measurements/control several times per year <i>and</i> the establishment of permanent physical barriers	Exclosure method
Depend	ence on infrastructure	
1	Independent of accessibility	
2	Relatively low dependence on accessibility	Estimation method
3	Low dependence on accessibility, but terrain should allow easy	Single-plot with or without area- based stop criterion, <i>N</i> -highest tree,
4	measurements on plot Same as 3, but terrain should be more homogeneous	k-tree, nearest-tree Cluster-plot with or without area- based stop criterion, k-cluster
5	Highly dependent on road/air accessibility	Exclosure method

can be calculated. In this case, later evaluations of the monitoring results or comparisons of the results over time cannot be regarded as robust. The extrapolation of values from completely sampled plots to a larger unit of area, e.g. a hectare, is easily possible when an area-based method has been used (see Table 1), due to easily calculable expansion factors (Kleinn and Vilčko, 2006b). However, if a stop criterion (e.g. measurements are stopped after n trees or only a fraction of the plot area is measured) is applied to reduce the effort and the measured part of the plot is not representative of the whole plot, an over- or underestimation may result (Reimoser et al., 2014; Rawinski, 2018) (Table 4). The spatial arrangement of the trees is also important in avoiding systematic bias, in

**Table 4**Grading and categorisation of data quality indicator parameters for each browsing-impact monitoring method.

Grade	Categorisation	Methods				
Suscept	ibility to measurement errors					
1	Methodology pre-determines a	k-tree				
	relatively low number of trees that					
	need to be measured					
2	Methodology pre-determines a	N-highest tree, k-cluster, Nearest-				
	relatively low number of trees that	tree, single-plot with area-based				
	need to be measured but several sub-	stop criterion				
	plots are involved <i>or</i> there are					
	additional selection criteria besides closeness to the plot centre that could					
	create strong biases when incorrectly					
	measured					
3	Methodology pre-determines a	Cluster-plot with area-based stop				
	reduced number of trees that need to	criterion; single-plot without a				
	be measured but nonetheless	stop criterion				
	includes several sub-plots, or the					
	methodology applies to a single plot					
	but does not pre-determine the					
	number of trees that need to be					
4	measured Methodology does not pre-determine	Cluster-plot without stop criterion				
7	the number of trees that need to be	exclosure method				
	measured and several sub-plots are	chelosure memou				
	involved					
5	Methodology based on estimations of	Estimation method				
	the browsing impact					
Method	lological accuracy					
1	Scientific consensus regarding a	Single-plot without a stop				
	method's estimation accuracy;	criterion; cluster-plot without a				
2	methodology produces objective data	stop criterion				
	Possible bias, as measured sub-plots might not be representative of the	Single-plot with area-based stop criterion, cluster plot with area-				
	whole plot	based stop criterion				
3	Intrinsic bias for calculating	Nearest-tree				
	regeneration density and the inability					
	to calculate browsing intensity (but					
	unbiased calculation of stocked area)					
	due to spatial irregularities of the					
	trees by a single estimator	At his house to have a factorial				
4	Intrinsic bias arising from several	<i>N</i> -highest tree, <i>k</i> -tree, <i>k</i> -cluster, exclosure method				
	estimators (density, browsing indicators, etc.) or due to a potential	CACIOSUI E III EHIOU				
	under-representation of rare species					
	and/or unknown legacy effects of					
	browsing					
5	Data acquisition is highly subjective	Estimation method				
	and hardly reproducible					
	hange prediction					
1	Change in the effect can be detected;					
	the same areas/trees are measured at every measurement period					
2	Changes in the effect can be detected	Single-plot with and without area				
	and measurements in the same area	based stop criterion, cluster-plot				
	are guaranteed (but not on the same	with and without area-based stop				
	trees, due to new trees or outgrowth)	criterion				
3	Changes in effect can only be	N-highest tree, $k$ -tree, $k$ -cluster,				
	estimated because potentially new	nearest-tree				
	trees are measured over time					
4	Does not allow a clear determination	Exclosure method				
	of browsing trends as changes cannot					
5	be attributed to ungulate impacts  Data are subjective and measurement	Estimation method				
J	of the same area and trees cannot be	Estillation method				
	or the same area and trees cannot be					

the case of irregularly spaced trees (Kupferschmid and Gmür, 2020). This holds true for methods based on fixed areas (in particular, with small plots) and especially for methods in which the density calculation is based on the distance to the plot centre of k tree. That is, if k+1 and not only k trees have been included, the distance to the plot centre may be the same, due to groups of regenerating trees, and the density will therefore be underestimated. Thus, for this parameter, categorisation reflects the

possibility of intrinsic bias arising after field measurements (Table 4).

3.3.3.3. Effect change prediction. For an optimal evaluation of monitoring results, the monitoring method should provide information not only on the current ungulate effect, but also on the change of the effect over time. For example, repeated measurements are crucial for detecting and evaluating the changes resulting from a browsing impact, e.g. in species composition. Therefore, the method should allow for repeated measurements of the same tree without influencing either its growth or other characteristics. The latter can also result from a monitoring method that indirectly affects plant growth, such as one that requires the placement of fences (Bergström and Edenius, 2003; Table 4).

#### 3.4. Final method-indicator matrix

The different monitoring methods and indicators were combined to form a matrix that allows evaluation of the various browsing-impact monitoring methods. Within the resulting method-indicator matrix (Table 5), each column represents a monitoring method identified in the literature search and each row reports the grade of the method for each of the above-described parameters for each indicator group. The parameters will differ in their relative importance depending on the management purpose. By altering the weighting of the different parameters, the matrix can be easily adjusted as needed. The following section provides an example of the derivation of the weights and the application of the method-indicator matrix.

#### 3.5. Example: selection of a monitoring method for German national parks

The method-indicator matrix was used to select the most suitable monitoring method for large-scale browsing monitoring in terrestrial German national parks. During a workshop held in 2019, the national park's wildlife management authorities identified the objectives of wildlife management and their requirements for a browsing-impact monitoring method. Discussions during the workshop were fundamental to the derivation of weights (1–4) for each of the indicators in the matrix, with higher weights reflecting a greater importance as identified by the wildlife management authorities.

Generally, the need for an effective browsing-impact monitoring system was highlighted by all of Germany's national parks. Within the

workshop, the advantages and disadvantages of the indicators, available resources as well as priorities were discussed. After all browsing indicators were presented, the national park representatives agreed that all indicator parameters were highly important and should be included in monitoring (weighting = 4). Specifically, among the performance indicators, disturbance of wildlife and dependence on infrastructure were identified as least important (weighting = 1), followed by expertise (weighting = 2), while expense was identified as important (weighting = 3), resulting in an average weighting of 1.8 for all performance indicators. Among the data quality indicators, the ability to detect changes in browsing over time was identified as the most important (weighting = 4), the possibility of intrinsic bias after field collection as relatively important (weighting = 3) and the susceptibility to measurement errors in the field as less important (weighting = 2), resulting in an overall weight of 3. Based on the weights added to the method-indicator matrix, the nearest-tree method scored highest, with a grade of 1.9, closely followed by the single plot with an area-based stop criterion, with a grade of 2.0, and the k-tree method, with a grade of 2.1 (Table 6).

An important advantage of the nearest-tree method is its relatively simple and bias-free estimation of the browsing indicators. Although the inclusion of height growth measurements was graded equally in the ktree and nearest-tree methods, as in both the measuring effort is less than in other methods, the nearest-tree method reduces structural bias caused by differences in regeneration density and tree diversity. This can be explained by the differences in the measured trees: while the nearest-tree method measures k-trees per tree species and per height class, the k-tree method measures the nearest x number of trees within a maximum search distance irrespective of tree height and species. Consequently, within the k-tree method there will be a high bias for rare species, depending on whether they are included or excluded by chance. To minimise this bias, more trees have to be measured in order to obtain information on different tree species and different height classes than in the nearest-tree method, increasing effort and personnel costs. In addition, compared to the nearest-tree method, the effort to measure the above-mentioned browsing indicator parameters on single plots is extremely high. In case of an area-stop criterion, the area size and therefore the effort are reduced but at the potential risk of a high over- or underestimation of browsing and of biases for rare species. However, the main disadvantage of the nearest-tree method according to most wildlife monitoring representatives is that exact browsing intensity cannot be

Table 5
Final method-indicator matrix. Each column represents one of the browsing-impact monitoring methods identified in the literature review and each row reports the respective grade for each of the parameters identified. For each of the indicator groups (browsing indicators, performance indicators and data quality indicators), an overall grade was calculated assuming equal weighting.

Parameters	Fixed a	area metho	ds				Fixed-count methods			
	Single-plot		Cluster-plot		Exclosure	Estimation	N-highest tree	K-tree	K-Cluster	Nearest-tree
	No	Stop	No	Stop						
Browsing indicators										
Regeneration density	1	1	2	2	2	5	4	3	4	2
Browsing incident	3	2	4	3	4	5	1	1	2	1
Within-tree browsing intensity	3	2	4	3	4	5	1	1	2	1
Height growth	4	2	5	3	4	5	3	1	4	1
Browsing-induced tree mortality	4	3	4	3	1	5	4	2	2	2
Average grade by equal weighting	3.0	2.0	3.8	2.8	3.0	5.0	2.6	1.6	2.8	1.4
Performance indicators										
Expense	3	2	4	3	5	1	2	2	3	2
Expertise	2	2	3	3	5	5	3	3	3	3
Disturbance of wildlife	3	2	4	3	5	1	2	2	3	2
Dependence on infrastructure	3	3	4	4	5	2	3	3	4	3
Average grade by equal weighting	2.8	2.3	3.8	3.3	5.0	2.3	2.5	2.5	3.3	2.5
Data quality indicators										
Susceptibility to measurement errors	3	2	4	3	4	5	2	1	2	2
Methodological accuracy	1	2	1	2	4	5	4	4	4	3
Effect change prediction	2	2	2	2	4	5	3	3	3	3
Average grade by equal weighting	2.0	2.0	2.3	2.3	4	5	3	2.7	3	2.7
Overall grade by equal weighting	2.7	2.1	3.4	2.8	3.9	4.1	2.7	2.2	3.0	2.1

**Table 6**Overview of the average grades for each browsing-impact monitoring method calculated for each of the indicator groups based on the individual weights assigned to each parameter. Grades were calculated as follows: Sum (grade parameter × weighting factor for each parameter)/Sum (weighting factors for all parameters).

Indicator group	dicator group Fixed area methods					Fixed-count methods				
	Single-plot		Cluster-plot		Exclosure	Estimation	N-highest tree	K-tree	K-Cluster	Nearest-tree
	No	Stop	No	Stop						
Browsing indicators	3.0	2.0	3.8	2.8	3.0	5.0	2.6	1.6	2.8	1.4
Performance indicators	2.7	2.1	3.7	3.1	5.0	2.3	2.4	2.4	3.1	2.4
Data quality indicators	1.9	2.0	2.1	2.2	4.0	5.0	3.1	2.9	3.1	2.8
Overall grade	2.7	2.0	3.3	2.7	3.6	4.5	2.7	2.1	2.9	1.9

calculated: instead, the proportion of the stocked area with browsed trees can be calculated, which is also important for silvicultural decisions. All wildlife monitoring representatives of the German terrestrial national parks agreed that information on rare species was more important for national parks than calculating browsing intensity and therefore chose the nearest-tree method for the implementation of browsing-impact monitoring in German terrestrial national parks.

#### 4. Discussion

Ungulate browsing often affects tree regeneration and thus prevents the achievement of economic or conservation goals. An assessment of the impact of browsing must have a sound scientific basis. However, while the importance of the indicators cited in this study is well-recognised, they have yet to be considered when planning a browsing-impact monitoring, either because managers are not aware of the respective parameters or because a lack of resources hinders their assessment. This study is the first to summarise current browsing-impact monitoring methods and associated indicators, including the advantages and disadvantages of those methods. The information was used to develop an evaluation matrix that facilitates the selection by forest managers of a scientifically appropriate method to measure ungulate browsing impact based on site-specific requirements and other constraints.

Several different approaches to continuous browsing-impact monitoring have been applied, with monitoring methods strongly differing within and between countries. For example, in Germany, the methods differ between German federal states, with little consensus regarding their use (Wotschikowsky, 2010). In the United Kingdom, browsing is monitored depending on the forest ownership structure, with no formal monitoring in privately owned forests (Reimoser and Putman, 2011). However, the diversity of monitoring methods prevents direct comparisons between areas (e.g. Reimoser et al., 2014), although the data are essential to an open and informed public debate about ungulate management and the associated trade-offs. The method-indicator matrix presented herein enables data comparability between monitoring methods, by allowing managers to easily identify methodological differences. As such, application of the method-indicator matrix supports the harmonization of browsing-impact monitoring across multiple areas.

For wildlife and forest managers, the choice of monitoring method must take into account local conditions and resources. While the decision-making benefits conferred by using the method-indicator matrix and thus allows a harmonization in the decision process, there is no universally appropriate method. In addition, single indicator parameters may be so important that their inclusion is an obvious choice. For example, in our case study of Germany's national parks, given the importance of height growth measurements and information on rare species, the nearest-tree method was selected, in which the nearest two trees per tree species and height class are measured. Furthermore, although most studies on the impact of ungulates on forest regeneration focus on browsing impact, bark-stripping and fraying can strongly influence the broader forest ecosystem as well. Bark-stripping strongly differs between tree species and forest stands but generally enables fungal infections, leading to growth reductions (Gill, 1992; Cukor et al., 2019), while fraying promotes tree mortality (Motta, 2003).

Consequently, any assessment of the overall impact of ungulates on forest ecosystems must include bark-stripping and fraying measurements. As fraying often affects trees within browsing range (Gill, 1992), its impact can be easily assessed during a browsing-impact assessment by using the k-tree or nearest tree method.

As stated by Dale and Beyeler (2001), a key challenge of monitoring programs is to find a mix of measures which give interpretable signals, can be used to track the ecological condition as at reasonable cost and cover the spectrum of ecological variation. Ideally, ecological indicators need to capture ecosystem complexity, are sufficiently sensitive to provide an early warning for change and should be easy and cost-effective to measure that allows them to be measured repeatedly (Noss, 1990; Dale and Beyeler, 2001). We believe we included a complete range of functional, structural and compositional indicators, identified through our literature review, necessary to assess ungulate browsing that form the basis for adaptive ungulate management. Even though the indicators included within this study are relatively easily measured and are sensitive to stresses on the system (Dale and Beyeler, 2001), they will not provide an explanation of the differences in ungulate browsing found over time or between different areas. Ungulate browsing is a multifactorial complex phenomenon where ungulate density estimates, ungulate community structure, vegetation cover, forest composition and light availability affect the incidence of browsing (Bergqvist et al., 2014; Churski et al., 2017; Kupferschmid et al., 2020). As the risk of browsing is related to both forest structure and ungulate community, forestry and wildlife management are intertwined. Consequently, browsing-impact monitoring is highly important to understand forest dynamics and to reduce browsing impacts.

In conclusion, in this study a scientific tool was created to aid in the selection of the most appropriate method of browsing-impact monitoring. The resulting method-indicator matrix, in which the advantages and disadvantages of each method are highlighted, can guide managers in their selection of the most appropriate method to measure the impact of ungulate browsing. Moreover, both weighting and grading can be adapted to local conditions as needed, to ensure the selection of the best browsing-impact monitoring method. Thus, our study enables a more scientifically based objectification of the methods used to assess the frequency of ungulate browsing, which has important management and conservation implications. Nonetheless, a truly objective assessment of the ungulate browsing impact on forest regeneration can only be obtained by including all of the browsing indicators considered in this study (e.g. Kupferschmid et al., 2022a). In addition, to serve as a monitoring tool for adaptive ungulate management, browsing inventories should be conducted regularly, and management targets should be clearly defined to allow comparison between different regions over time.

#### CRediT authorship contribution statement

Suzanne T.S. van Beeck Calkoen: Methodology, Validation, Writing – original draft. Jérôme Milch: Conceptualization, Methodology, Writing – original draft. Andrea D. Kupferschmid: Conceptualization, Methodology, Writing – review & editing. Christian Fiderer: Conceptualization, Funding acquisition, Methodology, Project administration, Writing – review & editing. Marco Heurich: Conceptualization, Funding

acquisition, Methodology, Supervision, 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://do i.org/10.1016/j.fecs.2023.100147.

#### References

- Abrams, M.D., Johnson, S.E., 2012. Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. J. Torrey Bot. Soc. 139, 167–180. https://doi.org/10.3159/torrey-d-11-00075.1.
- Andreasen, J.K., O'Neill, R.V., Noss, R., Slosser, N.C., 2001. Considerations for the development of a terrestrial index of ecological integrity. Ecol. Indicat. 1, 21–35. https://doi.org/10.1016/S1470-160X(01)00007-3.
- Angst, J.K., Kupferschmid, A.D., 2023. Assessing browsing impact in beech forests: the importance of tree responses after browsing. Diversity 15, 262.
- Apollonio, M., Andersen, R., Putman, R., 2010. European Ungulates and Their Management in the 21st Century. Cambridge University Press, UK.
- Archaux, F., Camaret, S., Dupouey, J.-L., Ulrich, E., Corcket, E., Bourjot, L., Brêthes, A., Chevalier, R., Dobremez, J.F., Dumas, Y., Dumé, G., Forêt, M., Forgeard, F., Gallet, M.L., Picard, J.F., Richard, F., Savoie, J.M., Seytre, L., Timbal, J., Touffet, J., 2009. Can we reliably estimate species richness with large plots? an assessment through calibration training. Plant Ecol. 203, 303–315. https://doi.org/10.1007/s11258-008-9551-6.
- Archaux, F., Gosselin, F., Bergès, L., Chevalier, R., 2006. Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. J. Veg. Sci. 17, 299–306. https://doi.org/10.1111/j.1654-1103.2006.tb02449.x.
- Avery, T.E., Burkhart, H.E., 2002. Forest Measurements, fifth ed. Waveland Press, Long Grove, Illinois.
- Bergqvist, G., Bergström, R., Wallgren, M., 2014. Recent browsing damage by moose on Scots pine, birch and aspen in young commercial forests – effects of forage availability, moose population density and site productivity. Silva Fenn. 48, 1077. https://doi.org/10.14214/sf.1077.
- Bergström, R., Edenius, L., 2003. From twigs to landscapes methods for studying ecological effects of forest ungulates. J. Nat. Conserv. 10, 203–211. https://doi.org/ 10.1078/1617-1381-00020.
- Bernes, C., Macura, B., Jonsson, B.G., Junninen, K., Müller, J., Sandström, J., Lohmus, A., Macdonald, E., 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. Environ. Evid. 7, 13. https://doi.org/10.1186/s13750-018-0125-3.
- Bonnot, N.C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J., Gehr, B., Heurich, M., Kjellander, P., Kröschel, M., Morellet, N., Sönnichsen, L., Hewison, A.J.M., 2020. Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. J. Anim. Ecol. 89, 132–145. https:// doi.org/10.1111/1365-2656.13161.
- Boulanger, V., Dupouey, J.-L., Archaux, F., Badeau, V., Baltzinger, C., Chevalier, R., Corcket, E., Dumas, Y., Forgeard, F., Mårell, A., Montpied, P., Paillet, Y., Picard, J.F., Saïd, S., Ulrich, E., 2018. Ungulates increase forest plant species richness to the benefit of non-forest specialists. Global Change Biol. 24, E485–E495. https://doi.org/10.1111/gcb.13899.
- Bryant, D.M., Ducey, M.J., Innes, J.C., Lee, T.D., Eckert, R.T., Zarin, D.J., 2005. Forest community analysis and the point-centered quarter method. Plant Ecol. 175, 193–203. https://doi.org/10.1007/s11258-005-0013-0.
- Cailleret, M., Heurich, M., Bugmann, H., 2014. Reduction in browsing intensity may not compensate climate change effects on tree species composition in the Bavarian Forest National Park. For. Ecol. Manag. 328, 179–192. https://doi.org/10.1016/ j.foreco.2014.05.030.
- Cantarello, E., Newton, A.C., 2008. Identifying cost-effective indicators to assess the conservation status of forested habitats in Natura 2000 sites. For. Ecol. Manag. 256, 815–826. https://doi.org/10.1016/J.FORECO.2008.05.031.
- Churski, M., Bubnicki, J.W., Jędrzejewska, B., Kuijper, D.P.J., Cromsigt, J.P.G.M., 2017. Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. New Phytol. 214, 158–168. https://doi.org/10.1111/nph.14345.
- Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725.

Cukor, J., Vacek, Z., Linda, R., Vacek, S., Marada, P., Simunek, V., Havránek, F., 2019.
Effects of bark stripping on timber production and structure of Norway spruce forests in relation to climatic factors. Forests 10, 320. https://doi.org/10.3390/f10040320.

- Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. Ecol. Indicat. 1, 3–10. https://doi.org/10.1016/S1470-160X(01)00003-6.
- Düggelin, C., Abegg, M., Bischof, S., Brändli, U.B., Cioldi, F., Fischer, C., Meile, R., 2020. Schweizerisches Landesforstinventar: Anleitung für die Feldaufnahmen der fünften Erhebung 2018-2026. Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL.
- Edenius, L., Danell, K., Nyquist, H., 1995. Effects of simulated moose browsing on growth, mortality, and fecundity in Scots pine: relations to plant productivity. Can. J. For. Res. 25, 529–535. https://doi.org/10.1139/x95-060.
- Eiberle, K., Nigg, H., 1987. Criteria for permissible browse impact on sycamore maple (Acer pseudoplatanus) in mountain forests. Experientia 43, 127–133. https://doi.org/ 10.1007/BF01942830.
- Endress, B.A., Naylor, B.J., Pekin, B.K., Wisdom, M.J., 2016. Aboveground and belowground mammalian herbivores regulate the demography of deciduous woody species in conifer forests. Ecosphere 7, 1–18. https://doi.org/10.1002/ecs2.1530.
- Failing, L., Gregory, R., 2003. Ten common mistakes in designing biodiversity indicators for forest policy. J. Environ. Manag. 68, 121–132. https://doi.org/10.1016/S0301-4797(03)00014-8.
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37, 550–556.
- Gill, R.M.A., 1992. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry 65, 363–388. https://doi.org/10.1093/forestry/ 65 4 363-a
- Gill, R.M.A., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74, 209–218. https://doi.org/10.1093/forestry/74.3.209.
- Gregoire, T.G., Valentine, H.T., 2007. Sampling Strategies for Natural Resources and the Environment. Chapman and Hall/CRC, New York.
- Habeck, C.W., Schultz, A.K., 2015. Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. AoB Plants 7, plv119. https://doi.org/10.1093/aobpla/plv119.
- Huber, M.O., Schwyzer, A., Kupferschmid, A.D., 2018. A comparison between plot-count and nearest-tree method in assessing tree regeneration features. Curr. Trends For. Res. https://doi.org/10.29011/2638-0013.100022.
- Keller, M., 2011. Swiss National Forest Inventory. Manual of the Field Survey 2004–2007. Swiss Federal Research Institute WSL Birmensdorf, p. 269.
- Kennedy, K.A., Addison, P.A., 1987. Some considerations for the use of visual estimates of plant cover in biomonitoring. J. Ecol. 75, 151. https://doi.org/10.2307/2260541.
- Kleinn, C., Vilcko, F., 2005. Ein Vergleich von zwei methodischen Konzepten für die Grundgesamtheit von Probeflächen bei Waldinventuren. Allgemeine Forst- und Jagdzeitung 176 (4), 68–74.
- Kleinn, C., Vilcko, F., 2006a. Design-unbiased estimation for point-to-tree distance sampling. Can. J. For. Res. 36, 1407–1414. https://doi.org/10.1139/X06-038.
- Kleinn, C., Vilčko, F., 2006b. A new empirical approach for estimation in k-tree sampling. For. Ecol. Manag. 237, 522–533. https://doi.org/10.1016/j.foreco.2006.09.072.
- Kramer, H., Alparslan, A., 2008. Leitfaden zur Waldmesslehre, 5. überarbeitetete Auflage. J.D. Sauerländer's Verlag, Frankfurt am Main.
- Krebs, C.J., 2014. Ecological Methodology. Benjamin Cummings, Addison Wesley, CA. Krueger, L.M., Peterson, C.J., Royo, A., Carson, W.P., 2009. Evaluating relationships among tree growth rate, shade tolerance, and browse tolerance following disturbance in an eastern deciduous forest. Can. J. For. Res. 39, 2460–2469.
- Kuijper, D.P.J., De Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., Jedrzejewska, B., 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. Ecography 36, 1263–1275.
- Kuijper, D.P.J., Jędrzejewska, B., Brzeziecki, B., Churski, M., Jedrzejewski, W., Zybura, H., 2010. Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. J. Veg. Sci. 21, 1082–1098. https://doi.org/10.1111/j.1654-1103.2010.01217.x.
- Kupferschmid, A.D., 2018. Selective browsing behaviour of ungulates influences the growth of *Abies alba* differently depending on forest type. For. Ecol. Manag. 429, 317–326. https://doi.org/10.1016/j.foreco.2018.06.046.
- Kupferschmid, A.D., Bugmann, H., 2013. Timing, light availability and vigour determine the response of *Abies alba* saplings to leader shoot browsing. Eur. J. For. Res. 132, 47–60. https://doi.org/10.1007/s10342-012-0653-2.
- Kupferschmid, A.D., Bütikofer, L., Hothorn, T., Schwyzer, A., Brang, P., 2020. Ungulate species and abundance as well as environmental factors determine the probability of terminal shoot browsing on temperate forest trees. Forests 11, 764. https://doi.org/ 10.3390/f11070764.
- Kupferschmid, A.D., Gmür, P.A., 2020. Methods for estimating the influence of browsing: comparison of the measurements on the k nearest trees with plot-count sampling. Schweiz. Z. Forstwes. 171, 69–78. https://doi.org/10.3188/szf.2020.0069.
- Kupferschmid, A.D., Greilsamer, R., Brang, P., Bugmann, H., 2022a. Assessment of the impact of ungulate browsing on tree regeneration. Anim. Nutr. IntechOpen. https:// doi.org/10.5772/intechopen.108667.
- Kupferschmid, A.D., Menendez, A., Sands, N., 2017. Compensation capacity of Central European tree species in response to leader shoot browsing. In: Menendez, A., Sands, N. (Eds.), Ungulates Evolution, Diversity and Ecology. Nova Science Publishers, USA.
- Kupferschmid, A.D., Seitz, L., Josi, J., Hothorn, T., 2022b. Assessment of Ungulate Effects on Trees in the Canton of Vaud. Swiss Federal Research Institute WSL, Birmensdor. https://doi.org/10.55419/wsl:31433.
- Kupferschmid, A.D., Wasem, U., Bugmann, H., 2015. Browsing regime and growth response of *Abies alba* saplings planted along light gradients. Eur. J. For. Res. 134, 75–87. https://doi.org/10.1007/s10342-014-0834-2.

Legg, C.J., Nagy, L., 2006. Why most conservation monitoring is, but need not be, a waste of time. J. Environ. Manag. 78, 194–199. https://doi.org/10.1016/ J.JENVMAN.2005.04.016.

- Lindenmayer, D.B., Likens, G.E., 2010. Effective Ecological Monitoring. Earthscan,
- Lynch, T.B., Rusydi, R., 1999. Distance sampling for forest inventory in Indonesian teak plantations. For. Ecol. Manag. 113, 215–221. https://doi.org/10.1016/S0378-1127(98)00427-7.
- Mandallaz, D., 2006. Sampling Techniques for Forest Inventories, Applied En. Chapman and Hall/CRC, Boca Raton.
- Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., Bugmann, H., 2018. Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. Sci. Rep. 8, 1–12. https://doi.org/10.1038/ s41598-018-23763-v.
- Morrison, L.W., 2016. Observer error in vegetation surveys: a review. J. Plant Ecol. 9, 367–379. https://doi.org/10.1093/jpe/rtv077.
- Motta, R., 2003. Ungulate impact on rowan (Sorbus aucuparia L.) and Norway spruce (Picea abies (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. For. Ecol. Manag. 181, 139–150. https://doi.org/10.1016/S0378-1127(03)00128-2.
- For. Ecol. Manag. 181, 139–150. https://doi.org/10.1016/S0378-1127(03)01128-2. Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends Ecol. Evol. 21, 668, 673
- Nomiya, H., Suzuki, W., Kanazashi, T., Shibata, M., Tanaka, H., Nakashizuka, T., 2003. The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. Plant Ecol. 164, 263–276. https://doi.org/10.1023/A:1021294021438.
- Nopp-Mayr, U., Schöll, E.M., Sachser, F., Reimoser, S., Reimoser, F., 2023. Does ungulate herbivory translate into diversity of woody plants? A long-term study in a montane forest ecosystem in Austria. Diversity 15, 165.
- Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conserv. Biol. 4, 355–364.
- Pellerin, M., Saïd, S., Richard, E., Hamann, J.L., Dubois-Coli, C., Hum, P., 2010. Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. For. Ecol. Manag. 260, 429–437. https://doi.org/ 10.1016/j.foreco.2010.04.031.
- Pelletier, F., 2014. Effects of tourist activities on ungulate behaviour in a mountain protected area. J. Mt. Ecol. 8, 15–19.
- Proffitt, K.M., Grigg, J.L., Hamlin, K.L., Garrott, R.A., 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. J. Wildl. Manag. 73, 345–356. https://doi.org/10.2193/2008-210.
- Ramezani, H., Grafström, A., Naghavi, H., Fallah, A., Shataee, S., Soosani, J., 2016. Evaluation of K-tree distance and fixed-sized plot sampling in zagros forests of western Iran. J. Agric. Sci. Technol. 18, 155–170.
- Rawinski, T.J., 2018. Monitoring White-tailed Deer Impacts: the Ten-Tallest Method. Newtown Square. PA. USA.
- Reimoser, F., Armstrong, H., Suchant, R., 1999. Measuring forest damage of ungulates: what should be considered. For. Ecol. Manag. 120, 47–58. https://doi.org/10.1016/ S0378-1127(98)00542-8.
- Reimoser, F., Putman, R., 2011. Impacts of wild ungulates on vegetation: costs and benefits. In: Putman, R., Apollonio, M., Andersen, R. (Eds.), Ungulate Management in Europe. Problems and Practices. Cambridge University Press, Cambridge, pp. 144–191.

- Reimoser, F., Reimoser, S., Schodterer, H., 2014. In: Erfassung und Beurteilung des Schalenwildeinflusses auf die Waldverjüngung Vergleich verschiedener Methoden des Wildeinfluss-Monitorings. ("WEM-methodenvergleich"). BFW Publishers, Vienna.
- Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manag. 181, 165–176. https://doi.org/10.1016/s0378-1127(03)00130-0.
- Royo, A.A., Collins, R., Adams, M.B., Kirschbaum, C., Carson, W.P., 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91, 93–105. https://doi.org/10.1890/08-1680.1.
- Rüegg, D., Nigg, H., 2003. Mehrstufige Verjüngungskontrollen und Grenzwerte für die Verbissintensität | Comparitive regeneration control and limiting value of browsing damage intensity. Schweiz. Z. Forstwes. 154, 314–321. https://doi.org/10.3188/ csf 2003.0314
- Schulze, E.D., Bouriaud, O., Wäldchen, J., Eisenhauer, N., Walentowski, H., Seele, C., Heinze, E., Pruschitzki, U., Danila, G., Marin, G., Hessenmöller, D., Bouriaud, L., Teodosiu, M., 2014. Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silvicultural management in Central and Southeastern Europe. Ann. For. Res. 57, 267–288. https://doi.org/10.15287/ afr.2014.273.
- Scott, C.T., 1998. Sampling methods for estimating change in forest resources. Ecol. Appl. 8, 228–233. https://doi.org/10.1890/1051-0761(1998)008[0228:SMFECI]2.0.CO;2.
- Simončič, T., Bončina, A., Jarni, K., Klopčič, M., 2019. Assessment of the long-term impact of deer on understory vegetation in mixed temperate forests. J. Veg. Sci. 30 (1) 108–120
- Smit, C., Putman, R., 2010. Large herbivores as 'environmental engineers. In: Putman, R., Apollonio, M., Andersen, R. (Eds.), Ungulate Management in Europe. Problems and Practices. Cambridge University Press, Cambridge, pp. 260–283.
- Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026.
- Stein, W.I., 1992. Regeneration Surveys and Evaluation. Forest Research Laboratory,
  Oregon State University. Corvallis, USA.
- Theuerkauf, J., Rouys, S., 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. For. Ecol. Manag. 256, 1335–1332
- Tremblay, J.-P., Huot, J., Potvin, F., 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. J. Appl. Ecol. 44, 552–562. https://doi.org/ 10.1111/j.1365-2664.2007.01290.x.
- Valente, A.M., Acevedo, P., Figueiredo, A.M., Fonseca, C., Torres, R.T., 2020.
  Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. Mamm. Rev. 50, 353–366. https://doi.org/10.1111/mam.12202.
- van Beeck Calkoen, S.T.S., Kreikenbohm, R., Kuijper, D.P.J., Heurich, M., 2021. Olfactory cues of large carnivores modify red deer behavior and browsing intensity. Behav. Ecol. 32, 982–992. https://doi.org/10.1093/beheco/arab071.
- Vowles, T., Molau, U., Lindstein, L., Molau, M., Bjorkm, R.G., 2016. The impact of shrub browsing by mountain hare and reindeer in subarctic Sweden. Plant Ecol. Divers. 9, 421–428. https://doi.org/10.1080/17550874.2016.1264017.
- Wotschikowsky, U., 2010. Ungulates ad their management in Germany. In: Apollonio, M., Andersen, R., Putman, R. (Eds.), European Ungulates and Their Management in the 21st Century. Cambridge University Press, Cambridge, p. 604.