



Number and height of unbrowsed saplings are more appropriate than the proportion of browsed saplings for predicting silvicultural regeneration success

Robert Hagen¹ · Norbert Kühl² · Marc Hanewinkel³ · Rudi Suchant⁴

Received: 31 July 2020 / Accepted: 13 January 2021 / Published online: 26 February 2021
© The Author(s) 2021

Abstract

• **Key message** The browsing level of oak (*Quercus petraea* and *Quercus robur*) and fir (*Abies alba*) provided only a rough estimate of the expected regeneration success. Thus, it cannot be recommended as a standard measurement to predict forest development, unless the number of saplings and the height of those saplings are considered.

• **Context** Browsing by large herbivores may affect regeneration success and forest development, with an impact that lasts for decades.

• **Aims** Whether the browsing level of a tree species can be used in forestry as a standard measure to assess whether the target values (for instance regeneration success) of highly selected tree species, such as oak (*Quercus petraea* (Mattuschka) Liebl., *Quercus robur* (L.)) and fir (*Abies alba* (Mill.)), will be reached is unclear and need specification.

• **Methods** In this study, 985 sampling plots (10 m²) in Southern Germany (Baden-Württemberg) containing browsed and unbrowsed oak and fir-saplings were analysed. Both the browsing level and a measure of the expected regeneration success that considered not only the sapling density but also different height classes (≤ 20 cm; 21–50 cm; 51–130 cm) were calculated.

• **Results** The use of the browsing level as a proxy for the expected regeneration success was statistically only partly justified. For fir the relationship between browsing level and expected regeneration success became even weaker for a new indicator variable which considers two height classes rather than one class for saplings exceeding 50 cm (51–80 cm and 81–130 cm).

• **Conclusion** According to these results, the browsing level cannot be recommended as a standard measurement and/or predictor of damage, unless the number of saplings and the height of those saplings are considered. Thus, in efforts to mitigate conflicts between foresters and hunters, a measurement is needed that addresses the successful establishment of a sufficient number of trees despite browsing, rather than the browsing of trees alone.

Keywords Oak · Fir · Roe deer · Damage

Handling Editor: Andreas Bolte

Contribution of the co-authors RH and RS conceived the ideas and designed the methodology. RH and NK were responsible for organising the field work. RH wrote the original draft. All authors contributed critically to the drafts and gave final approval for publication.

✉ Robert Hagen
hagen@izw-berlin.de

Norbert Kühl
Norbert.Kuehl@waldbau.uni-freiburg.de

Marc Hanewinkel
marc.hanewinkel@ife.uni-freiburg.de

Rudi Suchant
Rudi.Suchant@Forst.bwl.de

1 Introduction

That the browsing of large herbivores affects tree growth and the survival probability of single young trees is well-established (Kupferschmid and Bugmann 2008; Kupferschmid 2018). Foresters frequently suspect that browsing

¹ Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

² Chair of Silviculture, University of Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany

³ Forestry Economics and Planning, University of Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany

⁴ Forest Research Institute Baden-Württemberg, Wonnhaldestr. 4, 79100 Freiburg, Germany

by large herbivores such as roe deer (*Capreolus capreolus* (L.)) of trees undergoing natural regeneration causes damage that reduces their regeneration success and thus affects forest management objectives (Gill 1992; Reimoser and Gossow 1996). However, damage should be defined with respect to both a predefined management objective and comparisons of variables of interest with defined target values (Reimoser et al. 1997, 1999; Reimoser 2003). A target value for regeneration success might be (i) the minimum number of unbrowsed regeneration trees per area and tree height class that is needed for the establishment of a predefined stand (i.e. regeneration success, Beguin et al. 2016), (ii) a defined proportion of trees of one or more species (Reimoser et al. 1999) or (iii) the number of years needed until a germinated tree of a particular species reaches a height of 130 cm (Reimoser et al. 1999).

The presence of saplings of a certain height is a necessary precondition to reach a minimum number of unbrowsed regeneration trees per area and tree height. Whether seedlings and saplings of a certain tree species can be found at a certain forest site depends on a large number of factors, such as light availability (Weisberg et al. 2005; Kupferschmid et al. 2014), herbaceous vegetation cover, tree composition in the mature forest stand, soil fertility (Kuijper et al. 2010a) and the browsing level (Hidding et al. 2013; Kupferschmid et al. 2014). An impact of the browsing of large herbivores on tree regeneration is mostly confined to trees smaller than 130 cm (Zai 1964; Welch et al. 1992; Roth 1995). However, based on the results of long-term experiments, Pretzsch and co-authors (Pretzsch et al. 2019) were able to identify a relationship between the number of trees per ha that can be expected to emerge even in the absence of browsing and the diameters of those trees. Specifically, the logarithm of the number of trees per ha decreased with the logarithm of tree diameter (Pretzsch et al. 2019). Thus, major forest stands typically have a stem density of ~ 1000 per ha (1 stem per 10 m²) (McCarthy and Weetman 2007; Pretzsch et al. 2019), while the tree density in regeneration stands (diameter at 130 cm of < 1 cm) frequently exceed 100,000 trees per ha (Pretzsch et al. 2019).

Predicting the consequences of browsing for forestry is challenging (Clasen et al. 2015; Pretzsch et al. 2019) as forest development is a process that extends over decades and centuries. The question whether browsing by large herbivores adds to or compensates for losses occurring at later life stages, such as due to competition, insect

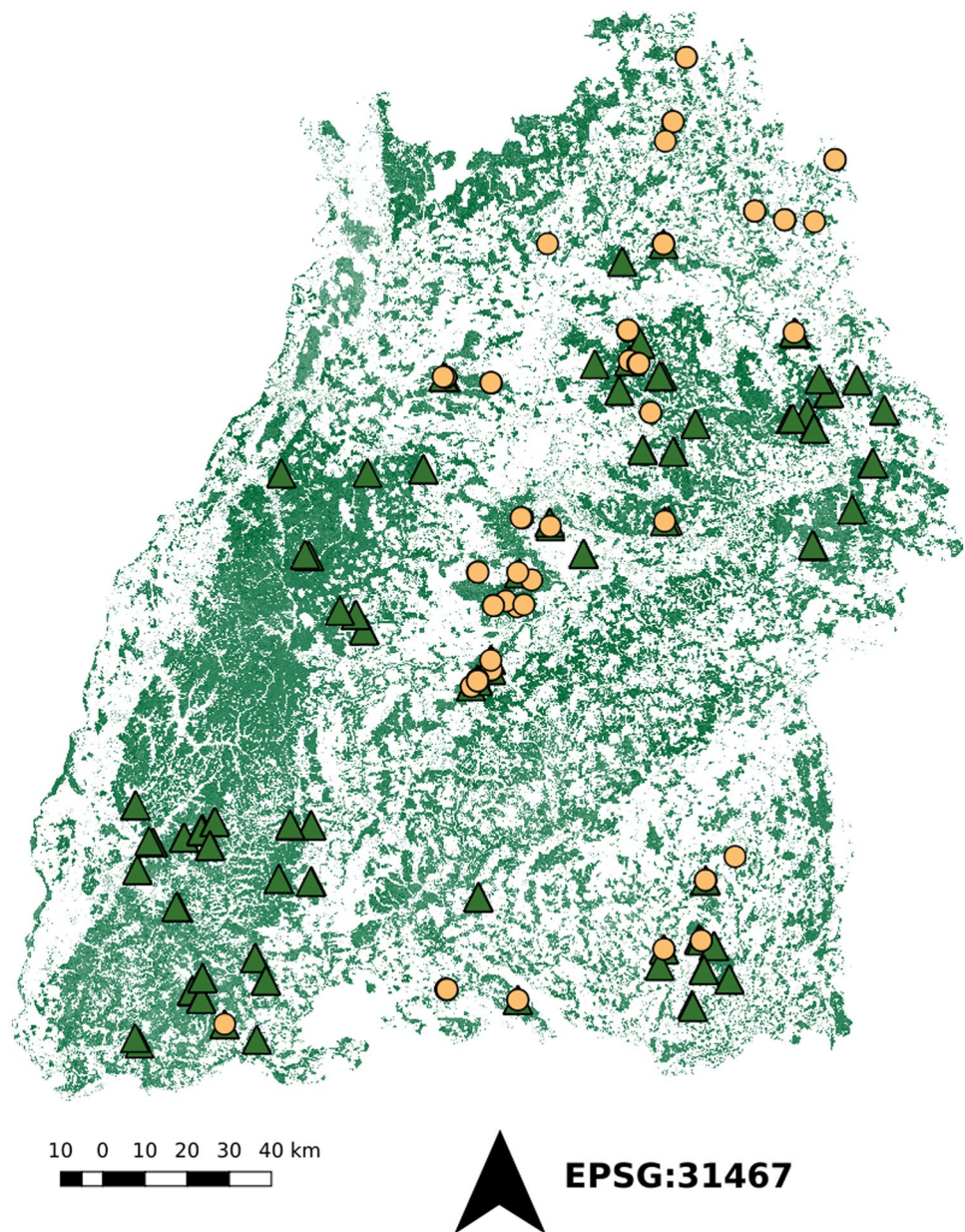
attacks or hurricanes, cannot be answered with certainty (Senn and Suter 2003; Coomes and Allen 2007). This conclusion is supported by the findings of a systematic review that investigated the effect of large herbivores on the abundance of tree saplings (Bernes et al. 2018). The authors found that the effect of browsing can vary strongly depending on the tree species considered. Consequently, using the browsing level as a reliable indicator of regeneration success has several drawbacks. Suchant and co-authors linked both the abundance of regeneration trees per height class and the browsing of trees to an expected regeneration success (FVA-approach—Appendix 1—cf. Suchant et al. 2012). In this context the FVA-approach may be applied to estimate the regeneration success of any indigenous tree species in the northern hemisphere. In this study, we calculated the expected regeneration success of oak (*Quercus petraea*, (*Mattuschka*) Liebl. and *Quercus robur* (L.)) and fir (*Abies alba* (Mill.)) and then compared the results with the browsing level. Ours is the first study to quantify the relationship of these two variables.

Based on a recent report by Hagen and Suchant (2020) showing that browsing level and sapling density are characterised by a spatial auto-correlation for a neighbourhood of 100 m, in the present study, we calculated Moran's *I* (Moran 1950) for neighbourhood distances of 50 m and 100 m (Appendix 2).

2 Data and methods

The study sites ($N = 98$) were located in the German federal state of Baden-Württemberg and consisted of forest patches with an expected natural regeneration of fir or oak (Hagen et al. 2019). In Baden-Württemberg, the browsing of young oaks and firs is mainly attributable to roe deer (*Capreolus capreolus*) (Hagen et al. 2019). Field surveys of the sites were conducted between 31.07.2017 and 29.09.2017 (deciduous forest) and between 26.03.2018 and 14.06.2018 (coniferous forest). The field surveys were timed taking into account the chance that the saplings would be browsed (oak in summer; fir in winter—cf. Odermatt 2014). A browsed tree was defined as a tree (height ≤ 130 cm) whose terminal bud was browsed during the last year. However, as the field surveys were timed according to the temporal prevalence of a browsing event, the browsing level mainly reflected seasonal browsing. Each study site contained 10 or more plots,

Fig. 1 Study sites containing saplings of oak (circles) and fir (triangles) where the number of saplings exceeded a defined minimum (4 trees [≤ 20 cm], 2 trees [21–50 cm] or 1 tree [51–130 cm]). The background shows the distribution of forest in Baden-Württemberg (Southern Germany). We used a geographic transformation to translate coordinates of the field survey from EPSG: 4326 to EPSG: 31467

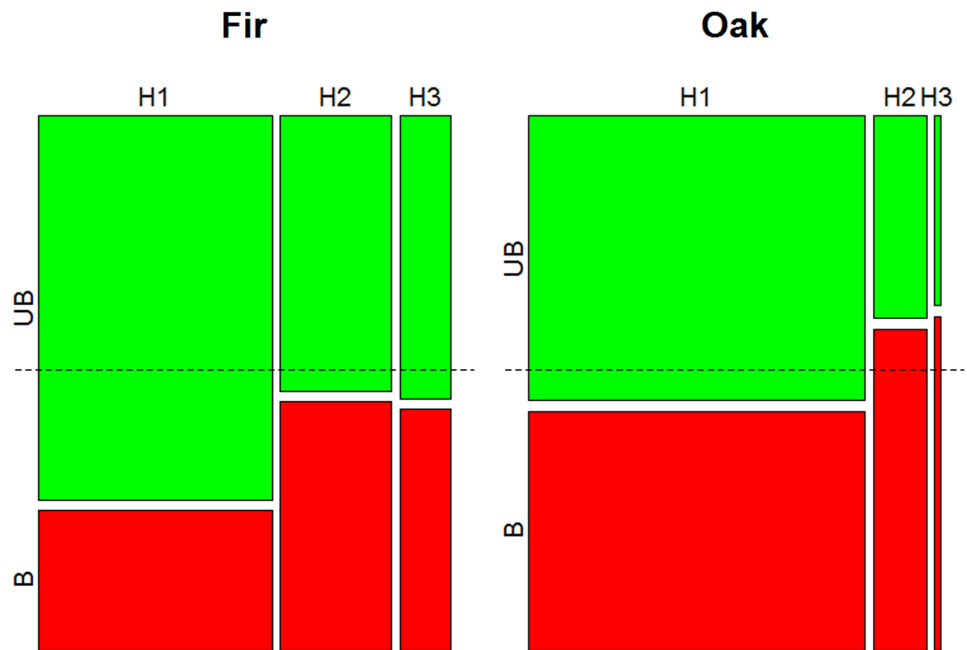


resulting in a total of 985 plots. The minimum distance between study sites was 1.4 km. The sampling plots in the study sites were circular. Analogous to Zai (1964) the area of each sapmling plots was 10 m^2 ($r = 1.79 \text{ m}$). The distance between two sampling plots was 25 m (+ 5 m). In each plot, the number of browsed and unbrowsed trees (height ≤ 130 cm) was documented (Hagen et al. 2021). Specifically, three different tree height classes were designated (1: ≤ 20 cm, 2: 21–50 cm, 3: 51–130 cm), which allowed the plot-specific browsing level to be linked to an expected regeneration success (FVA-approach—cf. Suchant et al. 2012). As the FVA approach has been

described only in German, we briefly present the basic aspects of its methodology in Appendix 1. The number of plots that fulfilled the criteria of the FVA approach (minimum number of regeneration trees per tree species) was 631 for fir and 197 for oak (see Fig. 1 for the spatial distribution of the study sites).

We then tested whether the browsing level differed according to the class value describing the regeneration success. This was done by applying a non-parametric correlation (Spearman), given that the distribution of the browsing level partly violates the assumption of a Gaussian distribution.

Fig. 2 Proportion of browsed (B) and unbrowsed (UB) fir and oak saplings according to the height class (H1 [< 20 cm], H2 [> 20 – 50 cm], H3 [> 50 – 130 cm]) of the saplings. The dashed horizontal line corresponds to a proportion of 50%, and the width of the bars is proportional to the number of saplings (fir: H1 [$N = 6340$], H2 [$N = 3022$], H3 [$N = 1369$]; oak: H1 [$N = 6640$], H2 [$N = 1046$], H3 [$N = 116$])



Statistical calculations were carried out using R version 3.4.4 (R Core Team 2018) and the R package spdep (Bivand et al. 2006).

3 Results

The overall browsing level for all 985 sampling plots was 0.35 (fir, $N = 10,731$) and 0.48 (oak, $N = 7802$), but browsing was not evenly distributed over the different height classes (Fig. 2) as fir and oak saplings smaller than 20 cm were less frequently browsed than saplings exceeding 20 cm.

A comparison between the browsing level and the expected regeneration success revealed a positive and

significant correlation between the browsing level and limitations of the regeneration success. The Spearman correlation coefficient ρ was 0.79 ($S = 8,652,700$, $p < 0.0001$) for fir and 0.71 ($S = 365,820$, $p < 0.0001$) for oak ($\rho^2_{\text{Fir}} = 0.63$; $\rho^2_{\text{Oak}} = 0.5$). Class values II, III, and IV were linked to a mean browsing level of 0.43, 0.64, and 0.8 for both tree species (see Table 1). Moreover, these three classes can be well distinguished according to the browsing level (Fig. 3).

For a plot with an oak browsing level of 0.8, the likelihood that it would be assigned class 4 (expected regeneration failure) was very high (Fig. 3). This assignment could be made without any specific knowledge about the height classes of the saplings. While the browsing level differed between sampling plots of class values II, III, and IV, the difference in the browsing level between class 0 and class I was small, which demonstrated the difficulty of linking a browsing level below 0.3 to any expected limitation of the regeneration success (Table 1 and Fig. 3).

Table 1 Comparison of the browsing level (bl) of fir and the expected regeneration success (cf. Fig. 3). Class 0 indicates that browsing is very unlikely to affect regeneration success and class IV that regeneration has failed due to browsing

| Class value (FVA approach) | 0 | I | II | III | IV |
|----------------------------|------|------|------|------|------|
| Fir | | | | | |
| Mean bl | 0.17 | 0.27 | 0.44 | 0.64 | 0.8 |
| 25% quantile of the bl | 0.0 | 0.14 | 0.33 | 0.53 | 0.63 |
| Median bl | 0.08 | 0.2 | 0.45 | 0.67 | 0.86 |
| 75% quantile of the bl | 0.31 | 0.33 | 0.54 | 0.75 | 1.0 |
| Oak | | | | | |
| Mean bl | 0.26 | 0.32 | 0.42 | 0.64 | 0.8 |
| 25% quantile of the bl | 0.0 | 0.17 | 0.3 | 0.56 | 0.68 |
| Median bl | 0.24 | 0.25 | 0.42 | 0.65 | 0.87 |
| 75% quantile of the bl | 0.48 | 0.48 | 0.51 | 0.74 | 1.0 |

4 Discussion

The correlation between the browsing level of oak and fir and the expected limitation of the regeneration success was significant and positive (cf. Fig. 3 and Table 2). This result partly reflects the process of assigning a class value according to the FVA-approach (Appendix 1, Figs. 5 and 6) and thus may support the conclusions of Hothorn and Müller (Hothorn and Müller 2010), who proposed the use of browsing level as a standard measure describing the effects on the development of tree saplings. However, the calculated ρ^2 values of 0.5 (oak) and 0.63

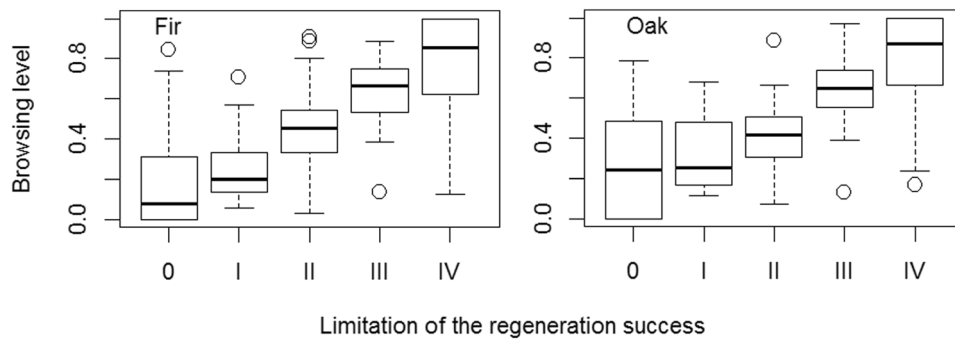


Fig. 3 Comparison of the browsing level of fir and oak and the regeneration success for 631 (fir) and 197 (oak) sampling plots (cf. Table 1). Please note the existence of sampling plots with a low

browsing level of less than 20% that were assigned to class 4 and sampling plots characterised by a high browsing level of more than 70% that were assigned to class 0

(fir) indicate that application of the browsing level as a proxy for the expected regeneration success is statistically only partly justified (by rule of thumb a value of $\rho^2 \geq 0.64$ is necessary). This restriction derives from the fact that plots characterised by a browsing level of < 20% were assigned to class IV (regeneration failure caused by browsing) and plots characterised by a high browsing level (> 70%) were assigned to class 0 (browsing is very unlikely to affect regeneration success) (Fig. 3). These differences between browsing level and regeneration success support our initial suspicion that the browsing level would not serve as a reliable indicator of forest development. Whether a specific browsing level will affect the target values depends on various factors, such as light conditions, soil conditions or local climate conditions (cf. Gerhardt et al. 2013). Moreover, application of the browsing level in the absence of knowledge about the sapling density considered (for instance 5, 10, 100 or any other number of saplings per 10 m²) or the height-class distribution of the saplings (Fig. 2) may lead to false conclusions about the possibility to reach silvicultural target values. For instance, it might reasonably be assumed that a documented browsing level of 60–80% will necessarily cause regeneration failure for any tree species, as the intense browsing will prohibit the regeneration of trees to a height of at least 130 cm (Weisberg et al. 2005). This assumption held either for an even-aged saplings ≤ 50 cm in height or for a constant browsing level for saplings in each height class. However, regeneration may occur

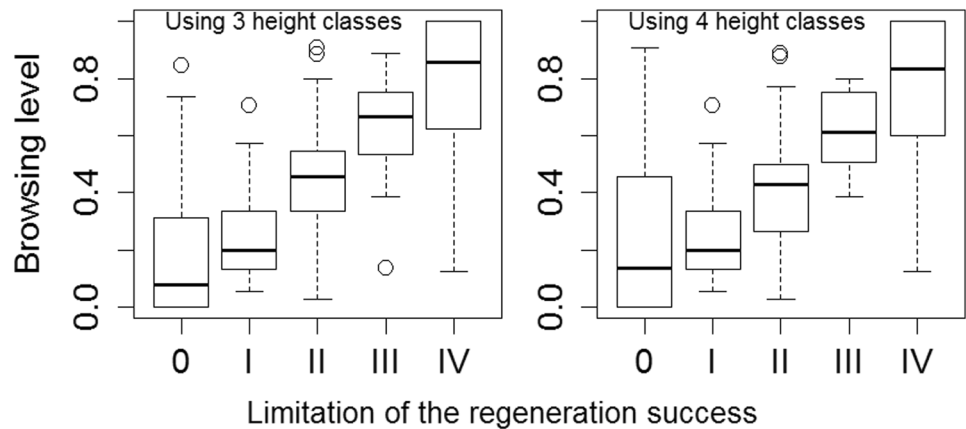
patchily (Yokozawa et al. 1999) or in waves (Wiegand et al. 1998) such that the number of saplings per height class may be approximated by a negative exponential distribution (Zai 1964; Coomes and Allen 2007; McCarthy and Weetman 2007). Thus, while browsing clearly affects forest development (Kuijper et al. 2010b; Pellerin et al. 2010; Hidding et al. 2012; Bernard et al. 2017; Bernes et al. 2018), a link between a certain browsing level and any future damage remains speculative. Long-term monitoring of the browsing level with respect to tree height may provide important insights into the spatio-temporal dynamics of both tree regeneration and herbivore activities (cf. Gill et al. 1996).

Our results showed that browsing was lowest on firs and oaks in height class 1 (smaller than 20 cm), the class with the largest number of saplings (Fig. 2). These results are in line with former results about tree height and browsing level (Zai 1964; Welch et al. 1992; Roth 1995; Chianucci et al. 2015). Welch and co-authors showed a higher browsing level (roe deer, red deer [*Cervus Elaphus* (L.)]) of trees (Sitka spruce) between 20 and 50 cm then of trees < 20 cm or > 50 cm in height (Welch et al. 1992). Their results are in line with the findings of both Zai (1964) and Roth (1995). Zai showed that saplings of fir with a height of 40–60 cm were those with the highest browsing level (roe deer), while in the study of Roth, browsing level was highest for trees with a height of 60–80 cm (Roth 1995). In a study about the browsing of oaks (*Quercus laevis* (Walt.)), Chianucci showed that the browsing level correlated negatively with the height of the saplings (Chianucci et al. 2015). All of these studies showed that for trees < 130 cm, a browsing level exceeding 60% may not endanger regeneration success when (i) browsing is concentrated on trees 20–80 cm in height and (ii) at least one unbrowsed tree per 10 m² exceeds a height of 80 cm. This conclusion is supported by the findings from some of our sampling plots. One

Table 2 Upper limit (UL) of the number of saplings within an area of 10 m² that were considered in an estimation of regeneration success

| | < 20 cm | 20–50 cm | 50–80 cm | 80–130 cm |
|---------------------|---------|----------|----------|-----------|
| UL coniferous trees | 12 | 6 | 2 | 1 |
| UL deciduous trees | 20 | 10 | 3 | 2 |

Fig. 4 Comparison of the browsing level of fir and the expected regeneration success using three height classes (FVA-approach) or by dividing height class 3 (51–130 cm) into two separate height classes (51–80 cm and 81–130 cm)



plot, for example, contained 13 firs smaller than 130 cm. Although 11 of the 13 trees had been browsed, the only tree taller than 50 cm (in fact, it was taller than 80 cm) was not affected by browsing.

Given the relationship between the number of trees per ha (saplings → major trees), tree height and browsing level, any measure aimed at providing an estimate of the regeneration success (such as the FVA-approach) should take into account both the total sapling number and the number of unbrowsed saplings, even though spatial independence cannot be expected. However, for fir and oak, we suggest an indicator that further determines sapling height for saplings exceeding 50 cm, including two separate height classes for sapling heights between 51 and 130 cm, such as 51–80 cm and 81–130 cm (Table 2). Regeneration success may then be estimated by applying the FVA-approach (Appendix 1) although the linear relationship between browsing level and expected regeneration success will likely become even weaker (Fig. 4).

However, variables trying to quantify the regeneration success are only partly suitable for predicting forest development (i.e. they cannot predict droughts, storm events, beetle attacks). Rather, variables that take into account sapling abundance and sapling height will be more appropriate than those based on the proportion of browsed trees in estimating the likelihood of reaching silvicultural target values.

5 Conclusion

The browsing level cannot be recommended as a predictor of both regeneration success and forest development unless the number of saplings and the height of those saplings are considered. Thus, in efforts to mitigate conflicts between foresters and hunters, a measurement is needed that addresses the successful establishment of a sufficient number of trees despite browsing, rather than the browsing of trees alone. The indicator variable introduced in this manuscript may serve as

such a measurement. It is based on the FVA-approach (Appendix 1) but considers two height classes rather than one class for saplings exceeding 50 cm (51–80 cm and 81–130 cm) and thus accounts for the circumstance that browsing of large herbivores on tree regeneration is mostly confined to trees smaller than 80 cm.

Appendix 1

The FVA approach has been applied in the Federal State of Baden-Württemberg since 2010. It links the seasonal browsing (last 6 months) to an expected regeneration success. The occurrence of a minimum number of saplings

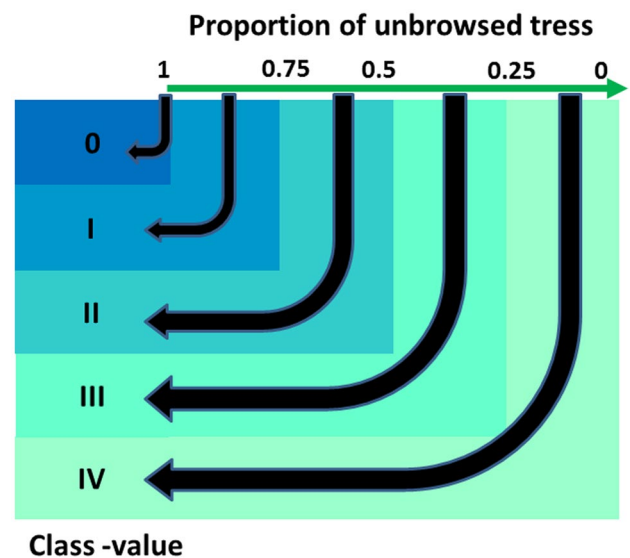
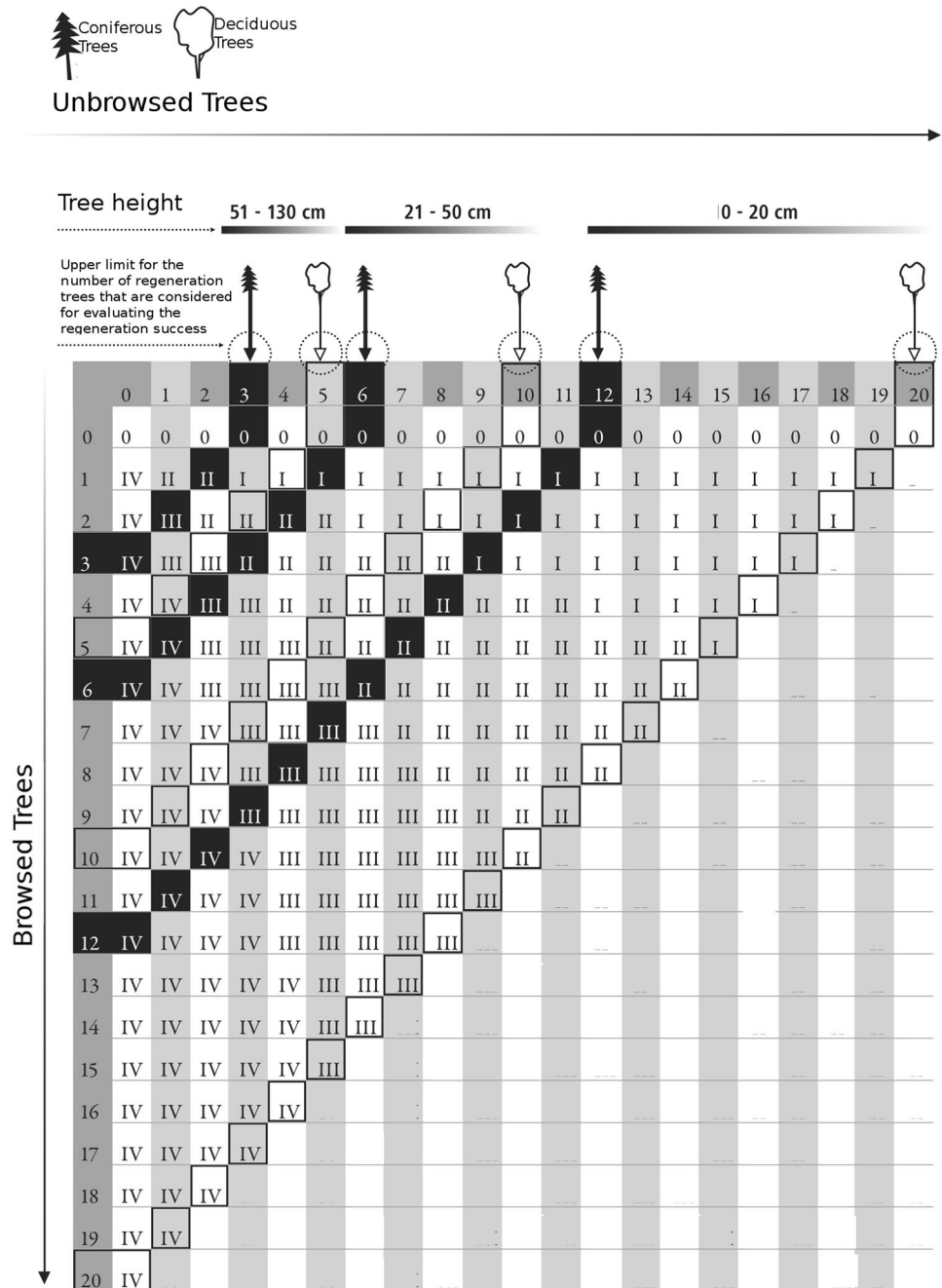


Fig. 5 Relationship between the class value (0, I, II, III, IV) representing the expected limitation in regeneration success and the proportion of unbrowsed trees (< 130 cm). Note that the assignments are only valid for sampling plots where the number of unbrowsed trees is below the upper limit defined in Table 3. If the number of unbrowsed trees exceeds the upper limit for this height class, then the plot is assigned class 0 (i.e. regeneration success is not endangered)

Fig. 6 Assignment of the class-value (0, I, II, III, IV) of the FVA-approach based on the number of browsed and unbrowsed trees per sampling plot (10 m²) and tree height (cf. Fig. 1). Class 0 indicates that browsing is very unlikely to affect regeneration success, while class IV that regeneration has failed due to browsing



per height class and per tree species is a necessary precondition for its application. The minimum number was defined according to Suchant et al. (2012) as:

4 trees (height class 1; ≤ 20 cm), 2 trees (height class 2; 21–50 cm) or 1 tree (height class 3; 51–130 cm).

Thus, only plots containing either 4 trees in the height ≤ 20 cm, 2 trees in the height 21 to ≤ 50 cm or 1 tree in the height 51 to ≤ 130 cm were used for further analyses.

On the basis of the number of browsed and unbrowsed trees, each sampling plot is assigned a class value (class

0–IV) representing the expected regeneration success. Class 0 means that browsing is very unlikely to affect regeneration success, and class IV that regeneration

Table 3 Upper limit (UL) of the number of saplings within an area of 10 m² that were considered in an estimation of regeneration success according to the FVA approach

| | Height class 1 | Height class 2 | Height class 3 |
|---------------------|----------------|----------------|----------------|
| UL coniferous trees | 12 | 6 | 3 |
| UL deciduous trees | 20 | 10 | 5 |

Table 4 Moran's I for a neighbourhood distance of 50 and 100 m (estimate I_{50} and estimate I_{100}) based on sampling plots for fir ($N = 631$) and oak ($N = 197$). Italic values indicate statistical significance under a global p value of 0.05

| | Browsing level | Number of saplings | Expected limitation of regeneration success |
|--------------------|--------------------|--------------------|---|
| Fir | | | |
| Estimate I_{50} | 0.41 | 0.3 | 0.3 |
| <i>P two sided</i> | <i>< 0.0001</i> | <i>< 0.0001</i> | <i>< 0.0001</i> |
| Estimate I_{100} | 0.34 | 0.24 | 0.25 |
| <i>P two sided</i> | <i>< 0.0001</i> | <i>< 0.0001</i> | <i>< 0.0001</i> |
| Oak | | | |
| Estimate I_{50} | 0.19 | 0.18 | 0.13 |
| <i>P two sided</i> | 0.03 | <i>0.003</i> | 0.11 |
| Estimate I_{100} | 0.18 | 0.19 | 0.09 |
| <i>P two sided</i> | 0.13 | 0.009 | 0.44 |

has failed due to browsing. The number of unbrowsed trees is counted for height classes 3, 2, and 1, starting at height class 3. If the number of tree saplings exceeds the required minimum, only this height class has to be evaluated. If the number of unbrowsed trees per 10 m² exceeds the upper limit for this height class (Table 3), then the plot is assigned class 0. Otherwise, the class value for deciduous and coniferous trees is assigned according to Fig. 5, assuming a linear relationship between browsing and limitations in regeneration success. The class values for different combinations of browsed and unbrowsed trees are provided in Fig. 6.

The definition of an upper limit per height class accounts for different sapling densities of deciduous and coniferous trees and further reflects that the number of trees per height class (reflected by the diameter) can be modelled by a negative exponential distribution. Thus, the meaning of browsing in the context of regeneration success differs according to tree height and tree species.

Appendix 2

In this study, data on sapling density and browsing level were analysed for three different height classes (H1: < 20 cm; H2: 20–50 cm; H3: 50–130 cm) using sampling plots separated by a distance of 25 m (+ 5 m). The study design allowed investigations of the spatial patterns of these variables even for a neighbourhood distance of less than 200 m or 100 m, the typical distances between sampling units in scientific investigations (cf. Hagen and Suchant 2020). In that study, a pattern of spatial-auto-correlation in sapling density and browsing level was determined for a neighbourhood distance of 100 m and 200 m for fir and 100 m for oak (positive association). Taking into account the differences in seed dispersal between fir and oak (fir seeds are wind dispersed while oak seeds either germinate in the direct neighbourhood of the parent tree

or are transported by birds or mammals), we expected (i) a spatial auto-correlation for the density of oak saplings at neighbourhood distances of 50 m and (ii) that the effect size of this auto-correlation will be larger for oak.

We calculated Moran's I for a predefined neighbourhood d_{nb} ($d_{nb} = 50$ m, 100 m) to test for spatial independence:

$$I = (N/W) * (\sum_i (\sum_j w_{ij}(x_i - x_{\text{mean}}))) / \sum_i (x_i - x_{\text{mean}})^2 \quad (1)$$

where N is the number of spatial units, x is the browsing level, x_{mean} is the mean browsing level, w_{ij} is the weight according to the defined neighbourhood ($w_{ij} = 0$ for $i = j$; $w_{ij} = 0$ for $d(i, j) > d_{nb}$) and W is the sum of all w_{ij} .

A calculated value of I significantly less or greater than 0 negated the hypothesis that the browsing of young trees (height ≤ 130 cm) is a spatially independent process. The Bonferroni correction was used to correct for multiple testing effects (global p value of 0.05).

The calculation of Moran's I showed that the browsing level of fir for one sampling plot correlated significantly with the browsing level of the surrounding sampling plots ($d_{nb} 50,100$), whereas the browsing level of oaks was not significant ($d_{nb} 50,100$). Although the index of the expected limitation of regeneration success showed spatial auto-correlation, the estimated Moran's I was lower for both tree species. The sapling density of oak and fir showed a significant spatial auto-correlation (Table 4).

The fact that the density of oak saplings showed a significant auto-correlation only for a neighbourhood distance of 100 m is consistent with the findings of Gotmark and Kiffer, who showed that oak saplings may be clumped at a very local level (Götmark and Kiffer 2014). Thus, taking differences in the seed dispersal of fir and oak into consideration, spatial auto-correlation for oak at a neighbourhood distance of 50 m and a larger effect size for oak were expected. In our study, the sapling density of oak (neighbourhood distances of 50 m) was indeed characterised by spatial auto-correlation

(positive association) (Table 4) but there was no support for a larger effect size, as the strength of the spatial auto-correlation was higher for fir (Table 4). Moreover, the browsing level of fir was characterised by a significant auto-correlation for neighbourhood distances of 50 m and 100 m, while the browsing level of oaks showed no significant spatial auto-correlation (neither for a neighbourhood distance of 50 m nor for a neighbourhood distance of 100 m). This result may reflect the assumption of Senn and Suter (2003), that at smaller scales the density of saplings varies more than that of large herbivores. The absence of a significant auto-correlation in the browsing level of oaks may also point to differences in the selection process of roe deer (Hagen et al. 2019). The home range size of roe deer is between 0.2 and 0.6 km² (Morellet et al. 2013; Richard et al. 2014; Lovari et al. 2017) and thus larger than the area defined by a neighbourhood distance of either 50 m or 100 m (area of 0.01 and 0.03 km² respectively), especially in the regions of Baden-Württemberg where oak regenerates naturally (cf. Hagen et al. 2019). However, an inability to detect a spatial auto-correlation for the browsing level of oak saplings may simply reflect the limited temporal and spatial dimensions of an annual field survey (cf. Hagen and Suchant 2020).

Acknowledgements We thank everyone who helped in sample collection, especially P. Bas Van der Lei and L. Schlageter. We also thank W. Ran for editorial support during the preparation of previous drafts of this manuscript and two anonymous reviewers and the editors for constructive comments.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability The datasets generated and/or analysed during the current study are available in the Zenodo repository, <http://doi.org/10.5281/zenodo.4435940>

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Beguín J, Tremblay J, Thiffault N et al (2016) Management of forest regeneration in boreal and temperate deer – forest systems: challenges, guidelines, and research gaps. *Ecosphere* 7:1–16. <https://doi.org/10.1002/ecs2.1488>
- Bernard M, Boulanger V, Dupouey JL et al (2017) Deer browsing promotes Norway spruce at the expense of silver fir in the forest regeneration phase. *For Ecol Manage* 400:269–277. <https://doi.org/10.1016/j.foreco.2017.05.040>
- Bernes C, Macura B, Jonsson BG et al (2018) Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review, BioMed Central
- Bivand R, Bernat A, Carvalho M et al (2006) The spdep package, version 0.3–13
- Chianucci F, Mattioli L, Amorini E et al (2015) Early and long-term impacts of browsing by roe deer in oak coppiced woods along a gradient of population density. *Ann Silv Res* 39:32–36. <https://doi.org/10.12899/asr-945>
- Clasen C, Heurich M, Glaesener L et al (2015) What factors affect the survival of tree saplings under browsing, and how can a loss of admixed tree species be forecast? *Ecol Modell* 305:1–9. <https://doi.org/10.1016/j.ecolmodel.2015.03.002>
- Coomes DA, Allen RB (2007) Mortality and tree-size distributions in natural mixed-age forests. *J Ecol* 95:27–40. <https://doi.org/10.1111/j.1365-2745.2006.01179.x>
- Gerhardt P, Arnold JM, Hackländer K, Hochbichler E (2013) Determinants of deer impact in European forests—a systematic literature analysis. *For Ecol Manage* 310:173–186. <https://doi.org/10.1016/j.foreco.2013.08.030>
- Gill R (1992) A review of damage by mammals in north temperate forests: 1. Deer *Forestry* 65:145–169
- Gill RMA, Johnson AL, Francis A et al (1996) Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. *For Ecol Manage* 127:31–41
- Götmark F, Kiffer C (2014) Regeneration of oaks (*Quercus robur*/Q. petraea) and three other tree species during long-term succession after catastrophic disturbance (windthrow). *Plant Ecol* 215:1067–1080. <https://doi.org/10.1007/s11258-014-0365-4>
- Hagen R, Kühl N, Kröschel M, Suchant R (2019) Verbiss an Tanne und Eiche in Baden-Württemberg : Ein Vergleich zwischen nadelbaum- und laubbaumdominierten Waldbeständen. *Allg Forst- und Jagdzeitung* 7/8:161–168. <https://doi.org/10.23765/afjz0002044>
- Hagen R, Suchant R (2020) Evidence of a spatial auto-correlation in the browsing level of four major European tree species *Ecol Evol* 1–11 <https://doi.org/10.1002/ece3.6577>
- Hagen R, Kühl N, Hanewinkel M, Suchant R (2021) Browsing of oak and fir saplings in Baden-Württemberg (Southern Germany) 2017/2018 Zenodo. V1. [dataset]. <http://doi.org/10.5281/zenodo.4435940>
- Hidding B, Tremblay JP, Côté SD (2013) A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology* 94:2852–2860. <https://doi.org/10.1890/12-2015.1>
- Hidding B, Tremblay JP, Côté SD (2012) Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities. *For Ecol Manage* 276:96–103. <https://doi.org/10.1016/j.foreco.2012.03.023>
- Hothorn T, Müller J (2010) Large-scale reduction of ungulate browsing by managed sport hunting. *For Ecol Manage* 260:1416–1423. <https://doi.org/10.1016/j.foreco.2010.07.019>
- Kuijper DPJ, Cromsigt JPGM, Jędrzejewska B et al (2010a) Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. *J Ecol* 98:888–899. <https://doi.org/10.1111/j.1365-2745.2010.01656.x>
- Kuijper DPJ, Jędrzejewska B, Brzeziecki B et al (2010b) 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 AD (2018) Selective browsing behaviour of ungulates influences the growth of *Abies alba* differently depending on forest type. *For Ecol Manage* 429:317–326. <https://doi.org/10.1016/j.foreco.2018.06.046>
- Kupferschmid AD, Bugmann H (2008) Ungulate browsing in winter reduces the growth of *Fraxinus* and *Acer* saplings in subsequent unbrowsed years. *Plant Ecol* 198:121–134. <https://doi.org/10.1007/s11258-007-9390-x>
- Kupferschmid AD, Wasem U, Bugmann H (2014) Light availability and ungulate browsing determine growth, height and mortality of *Abies alba* saplings. *For Ecol Manage* 318:359–369. <https://doi.org/10.1016/j.foreco.2014.01.027>
- Lovari S, Serrao G, Mori E (2017) Woodland features determining home range size of roe deer. *Behav Processes* 140:115–120. <https://doi.org/10.1016/j.beproc.2017.04.012>
- McCarthy JW, Weetman G (2007) Self-thinning dynamics in a balsam fir (*Abies balsamea* (L.) Mill.) insect-mediated boreal forest chronosequence. *For Ecol Manage* 241:295–309. <https://doi.org/10.1016/j.foreco.2007.01.001>
- Moran PAP (1950) Notes on continuous stochastic phenomena. *Biometrika* 37:17–23. <https://doi.org/10.1093/biomet/37.1-2.17>
- Morellet N, Bonenfant C, Börger L et al (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *J Anim Ecol* 82:1326–1339. <https://doi.org/10.1111/1365-2656.12105>
- Odermatt O (2014) Wann sind die kritischen Phasen? *Wald und Holz* 2/14:23–26
- Pellerin M, Saïd S, Richard E et al (2010) Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. *For Ecol Manage* 260:429–437. <https://doi.org/10.1016/j.foreco.2010.04.031>
- Pretzsch H, del Río M, Biber P et al (2019) Maintenance of long-term experiments for unique insights into forest growth dynamics and trends: review and perspectives. *Eur J For Res* 138:165–185. <https://doi.org/10.1007/s10342-018-1151-y>
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, //r-project.org/, May 2019
- Reimoser F (2003) Steering the impacts of ungulates on temperate forests. *J Nat Conserv* 10:243–252. <https://doi.org/10.1078/1617-1381-00024>
- Reimoser F, Armstrong H, Suchant R (1999) Measuring forest damage of ungulates: what should be considered. *For Ecol Manage* 120:47–58. [https://doi.org/10.1016/S0378-1127\(98\)00542-8](https://doi.org/10.1016/S0378-1127(98)00542-8)
- Reimoser F, Gossow H (1996) Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *For Ecol Manage* 88:107–119
- Reimoser F, Odermatt O, Roth R, Suchant R (1997) Die Beurteilung von Wildverbiss durch Soll-Ist-Vergleich. *Allg Forst und Jagdzeitung* 168:214–227
- Richard E, Saïd S, Hamann JL, Gaillard JM (2014) Daily, seasonal, and annual variations in individual home-range overlap of two sympatric species of deer. *Can J Zool* 92:853–859
- Roth R (1995) Einfluss des Rehwildes (*Capreolus capreolus* L., 1758) auf die Naturverjüngung von Mischwäldern. Albert-Ludwigs University Freiburg
- Senn J, Suter W (2003) Ungulate browsing on silver fir (*Abies alba*) in the Swiss Alps: beliefs in search of supporting data. *For Ecol Manage* 181:151–164
- Suchant R, Calabró S, Burghardt F (2012) FVA Verfahren. In: ForstBW (ed) Die Beurteilung von Verbiss in Naturverjüngungen, 2nd edn. p 102
- Weisberg PJ, Bonavia F, Bugmann H (2005) Modeling the interacting effects of browsing and shading on mountain forest tree regeneration (*Picea abies*). *Ecol Modell* 185:213–230. <https://doi.org/10.1016/j.ecolmodel.2004.12.004>
- Welch D, Staines BW, Scott D, French DD (1992) Leader browsing by red and roe deer on young sitka spruce trees in Western Scotland. II. Effects on growth and tree form. *Forestry* 65:309–330. <https://doi.org/10.1093/forestry/65.3.309>
- Wiegand T, Moloney KA, Milton SJ (1998) Population dynamics, disturbance, and pattern evolution: identifying the fundamental scales of organization in a model ecosystem. *Am Nat* 152:321–337. <https://doi.org/10.1086/286172>
- Yokozawa M, Kubota Y, Hara T (1999) Effects of competition mode on the spatial pattern dynamics of wave regeneration in subalpine tree stands. *Ecol Modell* 118:73–86. [https://doi.org/10.1016/S0304-3800\(99\)00050-2](https://doi.org/10.1016/S0304-3800(99)00050-2)
- Zai LE (1964) Untersuchungen über Methoden zur Beurteilung von Rehwildverbiss in Waldbeständen. Eidgenössische Technische Hochschule in Zürich