



## Veteran trees in decline: Stratified national monitoring of oaks in Norway

Rannveig M. Jacobsen<sup>a</sup>, Tone Birkemoe<sup>b</sup>, Marianne Evju<sup>a,\*</sup>, Olav Skarpaas<sup>c</sup>, Anne Sverdrup-Thygeson<sup>b</sup>

<sup>a</sup> Norwegian Institute for Nature Research, Sognsveien 68, 0855 Oslo, Norway

<sup>b</sup> Norwegian University of Life Sciences (NMBU), Faculty of Environmental Sciences and Natural Resource Management (MINA), P.O. Box 5003 NMBU, 1432 Aas, Norway

<sup>c</sup> Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway

### ARTICLE INFO

#### Keywords:

Quercus  
Ancient tree  
Tree inventory  
Monitoring  
Annual decline  
Biodiversity hotspot  
Heritage trees

### ABSTRACT

Old veteran trees function as biodiversity hotspots in both forests and open landscapes, and protecting such trees is an important measure to halt loss of biodiversity. Nevertheless, the number of veteran trees continues to decline worldwide, although estimates of this decline mainly stem from geographically restricted case studies. In Norway, veteran oak trees have received special protection since 2011 through the Norwegian Biodiversity Act, however, there is a lack of knowledge on status and trends for these trees. A national monitoring program was started in 2012, using a random, stratified sampling procedure. We use the data from the baseline survey and the first monitoring revisit to estimate the total number as well as mortality trends of veteran oaks in Norway. Further, we assess recruitment potential (in the baseline survey) and changes in variables describing ecological state such as regrowth.

The monitoring area covered the geographical distribution of oaks in Norway and was divided into > 200 000 plots of 500 × 500 m. A set of 500 monitoring plots were randomly selected from two strata: High probability plots (n = 100; plots with high probability of occurrence of veteran oaks), and Low probability plots (n = 400), using existing knowledge and databases. Plots were surveyed over a five year-period (2012–2016), with 20 HighProb-plots and 80 LowProb-plots each year. All veteran oaks that were observed during the baseline survey were revisited in 2019, three to seven years after they were initially registered. Tree absence and cause of death/change of ecological status was recorded. We estimated a total of 138 100 veteran oaks in Norway based on the baseline survey, of which 25 000 could be denoted “top quality oaks”. Based on the revisit, we estimated a loss of 7 600 veteran trees, i.e., an annual mortality rate of 1.2%. Recruitment oaks were present in most plots with veteran oaks, but recruitment into the veteran oak category is slow and unlikely to balance out the mortality rate. More precise estimates of recruitment should be prioritized in future monitoring. The estimate of 138 000 veteran oaks far exceeds the appr. 10 000 trees registered in the national database, and clearly demonstrates the need for continued mapping and monitoring to improve the foundation for a knowledge-based land management. Further, this short-term monitoring demonstrates the decline of this biodiversity hotspot and pivotal source of ecosystem functions, despite increased protection in recent years. Our results and conclusions are relevant also for veteran trees of other species than oak.

### 1. Introduction

Old trees function as biodiversity hotspots in both forests (Lie et al., 2009, Müller et al., 2014, Wetherbee et al., 2020) and open landscapes, such as agricultural areas and parks (Jonsell 2012, Gough et al., 2014, Parmain and Bouget 2018). Protecting and ensuring adequate recruitment of old trees is thereby an important measure to halt the global loss

of biodiversity (Lindenmayer and Laurance 2016, IPBES 2019).

With increasing age, a number of changes occur in the structure of a tree. A large diversity of microhabitats develops, such as dead branches in the canopy (Lie et al., 2009, Pilskog et al., 2016) and cavities in the wood (Müller et al., 2014, Taylor and Ranius 2014, Pilskog et al., 2020), which are associated with specialized and often rare species. In oaks (*Quercus robur* or *Q. petraea*) for instance, hollows primarily develop in

\* Corresponding author.

E-mail address: [marianne.evju@nina.no](mailto:marianne.evju@nina.no) (M. Evju).

<https://doi.org/10.1016/j.foreco.2022.120624>

Received 13 September 2022; Received in revised form 30 October 2022; Accepted 1 November 2022

Available online 9 November 2022

0378-1127/© 2022 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

trees older than 200 years (Ranius et al., 2009a). The bark structure and chemical composition also changes with age; the bark gradually goes from being smooth to becoming coarse, often with deep crevices that provide habitat for rare species of lichen and insects (Bates and Brown 1981, Ranius et al., 2008, Nordén et al., 2018, Pilskog et al., 2020).

The high species richness associated with large, old trees has also been shown to promote functional diversity (Wetherbee et al., 2020). Large, old trees are keystone structures in ecosystems, with a disproportionately high contribution to several ecological functions such as fruit and seed production, provision of microhabitats, nitrogen fixation and carbon sequestration and storage (Lindenmayer et al., 2014, Gilhen-Baker et al., 2022). In urban settings, such trees can provide cities with ecosystem services such as cooling through shade and transpiration, removing air pollutants such as ozone and reducing flash flooding (Livesley et al., 2016). Trees in urban parks have also been found to positively affect people's well-being (Parra-Saldívar et al., 2020), and old trees can have significant cultural value (Blicharska and Mikusiński 2014, Gilhen-Baker et al., 2022), as exemplified by the Major Oak (*Quercus robur*) in Sherwood Forest in Great Britain, probably the most visited tree in the country (Nolan et al., 2020).

In this study, we use the term veteran trees to denote trees of particularly large size or with "veteran" qualities such as hollows (see definition in the methods sections), without specific requirements for tree age due to the difficulties of assessing age in the field. Size is often used as a proxy for age in defining veteran trees, usually defined as diameter or circumference at breast height (Lindenmayer and Laurance 2016). Though large young trees cannot fill the ecological role of large old trees (Lindenmayer et al., 2014), several studies have found positive effects of tree size on associated species richness, abundance or occurrence of rare species, especially for invertebrates and epiphytes (Ranius et al., 2008, Lie et al., 2009, Gough et al., 2014, Pilskog et al., 2016).

Despite the proven value of veteran trees for biodiversity, ecosystem functions and cultural heritage, numbers of veteran trees continue to decline worldwide (e.g., Laurance et al., 2000, Lindenmayer et al., 2014, Liu et al., 2019, Nolan et al., 2020). For instance, data from the Swedish National Forest Inventory for a study area in Norrbotten has shown that approximately 70% of the trees older than 160 years disappeared between 1926 and 1996, and the number of Scots pine older than 400 years had declined from an estimated 1 million to none (Andersson and Östlund 2004). Other studies based on forest inventory data at national and continent-wide scales indicate that also large trees (age and size are, naturally, often connected) are on the increase, at least in forests (Faison 2014, Henttonen et al., 2019), but even Henttonen et al., 2019 found no such increase for the very largest trees (>60 cm dbh), and a clear decline of old (>150 yrs) broadleaved trees was observed from the the 1970 s to the 2010 s. Further, simulation studies estimate continued dramatic declines in number of large trees over the next decades, both in urban (Le Roux et al., 2014) and rural areas (Gibbons et al., 2008). However, most estimates of veteran tree decline stem from case studies at small spatial scales, while the few national datasets for veteran trees are rarely obtained systematically for the whole country (e.g., Liu et al., 2019, Nolan et al., 2020).

For instance, The Ancient Tree Inventory in Great Britain, while a valuable source of information with 169 967 tree records, is based on citizen science and therefore strongly influenced by sampling bias, which complicates estimation of total number of trees and distribution modelling (Nolan et al., 2020). The distribution of veteran trees is frequently an outcome of natural and human influences interacting at varying spatial and temporal scales (Lindenmayer and Laurance 2016, Skarpaas et al., 2017), increasing the need for statistically sound monitoring (Boutin et al., 2009; Lindenmayer and Likens 2010). However, to provide unbiased and precise estimates for rare events, such as veteran tree occurrences, is challenging (Yoccoz et al., 2001, Dixon et al. 2005). Furthermore, there is a need for systematic, repeated monitoring of veteran trees to enable assessment of the effect of measures taken to protect this valuable habitat, thereby allowing for adaptive

management.

In Norway, veteran oaks (*Quercus robur* and *Q. petraea*) outside forest have received special protection since 2011 through the Norwegian Biodiversity Act (see Box 1). Oak trees host a particularly high number of species, including many specialists, in comparison with other tree species in Northern Europe (Jonsell et al., 1998, Sverdrup-Thygeson et al., 2011, Tingstad et al., 2018, Sundberg et al., 2019). In part, this high biodiversity is linked to the longevity of oak trees (Ranius et al., 2009b, Drobyshv and Niklasson 2010). At present, oak represents a very small proportion of the forested area in Norway (Svensson et al., 2021), but historically there were larger oak forests in southern Norway. In the 1500 s, a demand for high quality oak timber for ship building, combined with the introduction of river sawmills to Norway lead to intensive logging of oak, which might influence species distributions even today (Pilskog et al., 2018).

The present trend in the number of veteran oaks in Norway is unknown, though there are indications of a continued decline (Sverdrup-Thygeson et al., 2014). To alleviate this lack of knowledge, a national monitoring program for veteran oaks was initiated in 2010 and formally started in 2012. The program applies a random, stratified sampling procedure using existing information on the probability of veteran oak occurrence to define sampling strata of high and low probability veteran oak occurrence (cf. Dixon et al., 2005), sampling the entire distribution area of oak in Norway. The monitoring thus provides data suitable for estimates of total abundance of veteran oaks in Norway, current trends for mortality and potential for recruitment, and – in time – also the effect of protection measures such as the Norwegian Biodiversity Act. This study presents the design of the Norwegian veteran oak monitoring and the results from the baseline survey and subsequent first monitoring revisit. Specifically, we used this data to estimate: (i) total number of veteran oaks in Norway, (ii) total number of veteran oaks covered by Norwegian legislation (as a 'selected habitat type', see Box 1, or as situated in nature reserves), and (iii) mortality trend for veteran oaks in Norway. Further, we assessed (iv) the recruitment potential for veteran oaks in Norway, and (v) changes in the state variable (regrowth of shrubs and trees around oaks). We also assessed the monitoring program design according to precision of estimates and detectable change. Ultimately, we ask whether the number of veteran oaks in Norway is still declining, despite increased protection in recent years.

## 2. Methods

### 2.1. Monitoring area

Monitoring was restricted to the distribution area of oak in Norway, which was delimited by registered occurrence of oak and elevation as follows: The relevant monitoring area only included municipalities with a minimum of two occurrences of oaks registered either in the national species observation database (<https://artskart.artsdatabanken.no>, accessed May 2012) or registered occurrences of veteran oaks or nature types that typically include veteran oaks (in the database Naturbase, <https://kart.naturbase.no>, accessed May 2010). Relevant area in these municipalities was further restricted to land area below 400 m.a.s.l. The resulting relevant area for monitoring of veteran oaks covered 41 000 km<sup>2</sup> (Fig. 1).

### 2.2. Monitoring plots

The monitoring area was divided into 200 472 plots of 500 × 500 m<sup>2</sup>, following the nation-wide grid net from Statistics Norway (Strand et al., 2009). We stratified the dataset into plots with high probability (High-Prob) and low probability (LowProb) of occurrence of veteran oaks, based on existing knowledge (see Appendix A). Such stratification increases the precision of the estimated probability by removing the variability between strata (cf. Dixon et al., 2005). A pilot study surveying 36 HighProb-plots and 96 LowProb-plots used distribution

**Box 1**

Definition of veteran oaks in this study.

We define veteran oaks as oak trees (*Quercus robur* and *Q. petraea*) with a circumference of at least 200 cm (diameter > 62 cm) at breast height (130 cm above ground level), or with a circumference of at least 95 cm (diameter > 30 cm) and a visible hollow (where the interior of the hollow is larger than the opening, and the opening has a diameter of more than 5 cm). This definition is in accordance with the Norwegian Biodiversity Act (Lovdata 2011).

The special protection outside of nature reserves (called 'selected habitat type', 'utvalgt naturtype' in Norwegian) of veteran oaks only extends to veteran oaks outside productive forest and veteran oaks no further than 20 m within productive forest (measured from a border between open landscape and productive forest). Productive forest is defined as forested areas that can produce a minimum of 1 m<sup>3</sup> timber per hectare per year. However, all veteran oaks, regardless of surroundings, are registered in the Norwegian national monitoring presented here.

modelling to show that though likelihood of encountering veteran oaks was low across the landscape, the odds were > 300 times higher in certain areas (Skarpaas et al., 2017). Simulations showed that an over-representation of HighProb-plots in the monitoring program was preferable to allow modelling not only of veteran oak occurrence, but also of variables describing condition of the veteran oaks (Sverdrup-Thygeson et al., 2013, see Appendix A for details). Therefore, although less than 2% of the 200 472 plots were categorized as HighProb-plots, 20% of the plots included in the monitoring were HighProb-plots.

The baseline survey covered 500 plots over five years (2012–2016), wherein 20 HighProb-plots and 80 LowProb-plots were surveyed each year. Aerial photos of all plots were investigated prior to field visits, and plots where veteran oaks obviously could not occur (e.g., plots without trees) were not visited in field (this applied to 58 plots in total). All other plots were visited by field workers.

### 2.3. Registrations per plot

Field workers were instructed to survey each plot, thoroughly enough to discover all veteran oaks and most recruitment oaks, using line transects. Thus, field workers could adapt the effort to the terrain and vegetation of each plot, which varied considerably. Recruitment oaks were registered as number of small oaks (diameter at breast height (dbh) 10–<40 cm) and number of medium oaks (dbh 40–<63 cm) in the plot, with exact numbers from one to nine occurrences in total, and intervals for larger numbers (10–49, 50–99 and > 100). All veteran oaks (see Box 1 for definition) in the plots were counted and described.

### 2.4. Registrations per veteran oak

For each veteran oak, field workers collected coordinates and recorded the following variables (Appendix table B1): tree circumference, tree vitality, tree shape, bark type, size and placement of hollows, if present, and moss cover at the trunk. They recorded surrounding regrowth from shrubs and trees and assessed whether the tree would benefit from management such as crown stabilizing or removal of encroaching vegetation. Finally, the field workers assigned a biodiversity value of the tree according to three predefined categories (Appendix table B1). The top category and highest assumed value for biodiversity was ascribed to oaks that were likely to be of great age and to function as habitat for threatened species, based on qualities such as hollows with likelihood of high volumes of wood mold, coarse bark and large circumference. We refer to these trees as “top quality” veteran oaks. Data on oak coordinates and variables were uploaded to the Norwegian national database for areas with special nature values (Naturbase, <https://kart.naturbase.no>).

### 2.5. First monitoring revisit

All veteran oaks that were registered during the baseline survey were revisited in 2019, three to seven years after they were initially

registered. All variables describing the veteran trees were registered again (i.e. variables in Appendix table B1), and two additional variables were added:

- Tree present/absent: defined by following categories; (1) alive, (2) on the ground, (3) trunk partially left standing, (4) high stump, (5) completely gone.

- Cause of death/changed status (included fallen down/broken): defined by the following categories; (1) natural causes, (2) land use changes, (3) logged/felled.

To be able to revisit all veteran oaks registered during the five year baseline survey within a single year, field workers did not survey the entire plot. Thus, potential recruitment of small- or medium sized oaks into the category of veteran oaks, by increase in diameter or development of hollows since the baseline survey, was not registered during the revisit in 2019. Due to the slow process of oak growth and cavity formation (Ranius et al. 2009a), we do not expect that many, if any, new veteran oaks would have been registered in the plots only three to seven years after the initial visit.

During the revisit, 23 veteran oaks could not be found at all. That trees were not found, not even a trace such as a stump, could be due to poor coordinate precision, difficult terrain and/or difficulty in recognizing the tree. We therefore did not assume that these trees had been lost.

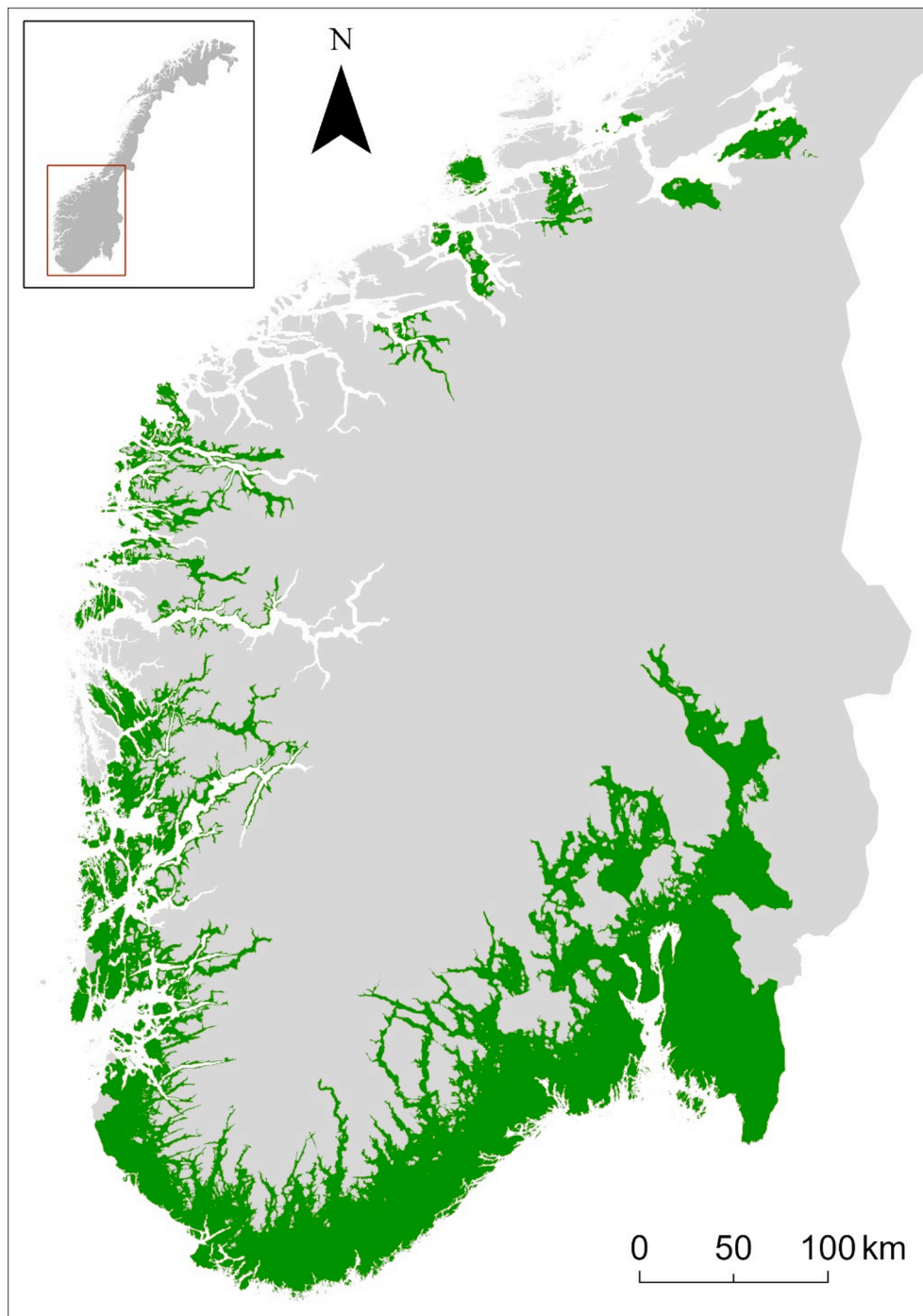
### 2.6. Statistical analysis

The total number of veteran oaks in Norway was estimated as follows; (average number of veteran oaks per HighProb-plot × total number of HighProb-plots in Norway) + (average number of veteran oaks per LowProb-plot × total number of LowProb-plots in Norway).

We resampled the data and estimated total number of veteran oaks 2000 times (each time sampling 100 HighProb-plots and 400 LowProb-plots, with replacement), to calculate the 95% confidence interval for the mean estimate. Total number of veteran oaks and of “top quality” veteran oaks was estimated by this manner based on data from the first monitoring period, and then again based on the adjusted data from the revisit.

Total number of veteran oaks covered by the Norwegian Biodiversity Act or occurring in nature reserves was estimated in the same manner, based on occurrence of the veteran oaks registered during the first monitoring period in nature reserves (as registered in <https://kartkatalog.miljodirektoratet.no/dataset/Details/0>, accessed October 2017) or outside (or at most 20 m within the edge) of productive forest (see Box 1, as registered in the Land Cover map AR5; Ahlstrøm et al., 2019, accessed October 2017).

The difference in estimated total number of veteran oaks from the baseline survey (first period) to the revisit (last period) was used to estimate the annual percent change by the following formula;



**Fig. 1.** The Norwegian national oak monitoring was restricted to the green area, which was delimited as described in the methods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$$\text{Annual\%change} = \left( \frac{\text{Numberforthe\textit{lastperiod}}}{\text{Numberforthe\textit{firstperiod}}^{\frac{1}{\text{Yearsdifference}} - 1}} - 1 \right) * 100$$

Since the baseline survey stretched over five years, and we used the estimated total number of trees based on these five years' collection of data, there was no true knowledge of *when* trees were lost, and thus difficult to calculate precise annual percent change. We solved this by assuming five scenarios: all lost trees were lost in 2012 (after the first year of the baseline survey), or in 2013, 2014, 2015, 2016. These scenarios gave a range of annual decline estimates.

Precision and detectable change for variable estimates based on the monitoring data was estimated by resampling ( $n = 2000$ ) both fewer

plots ((500) and double (1000) the number of plots included in the original monitoring program, to test the effect of number of monitored plots. Resampled plots were always distributed with 20% HighProb-plots and 80% LowProb-plots, and variable estimates were weighted based on the total number of HighProb- and LowProb-plots in Norway, as for the estimates of total number of veteran oaks. Detectable change was estimated with the function `power.t.test`, with power at 80%.

All analyses were conducted in R (several versions used; [R Core Team 2021](#)).

### 3. Results

During the baseline survey, 657 veteran oaks were registered in 114 of the 500 plots (Sverdrup-Thygeson et al 2018), i.e., 77% of the plots had no veteran oaks (Fig. 2). Of the 114 plots with oaks, 38 plots had one veteran oak, 60 plots had between two and ten veteran oaks, while 16 plots had more than ten veteran oaks (with a maximum of 56 veteran oaks in one plot). Veteran oaks occurred in 61% of the HighProb-plots, while there were veteran oaks in only 13% of the LowProb-plots. Ninety-five of the veteran oaks were considered “top quality”, i.e., having attributes associated with especially great age and high likelihood of occurrence of threatened species.

A total of 34 trees were recorded as fallen or cut down during the first monitoring revisit. Approximately half of the lost trees had clearly died due to human activities (15 of 34), such as logging or land use change, including eight trees covered by the Norwegian Biodiversity Act and one tree within a nature reserve. In total, two veteran oaks within nature reserves and 15 veteran oaks covered by the Act had been lost since the baseline survey. Five of the 95 “top quality” veteran oaks registered during the baseline survey had fallen or been cut down by 2019.

#### 3.1. Estimates for Norway

Based on data from the baseline survey, 138 100 veteran oaks were

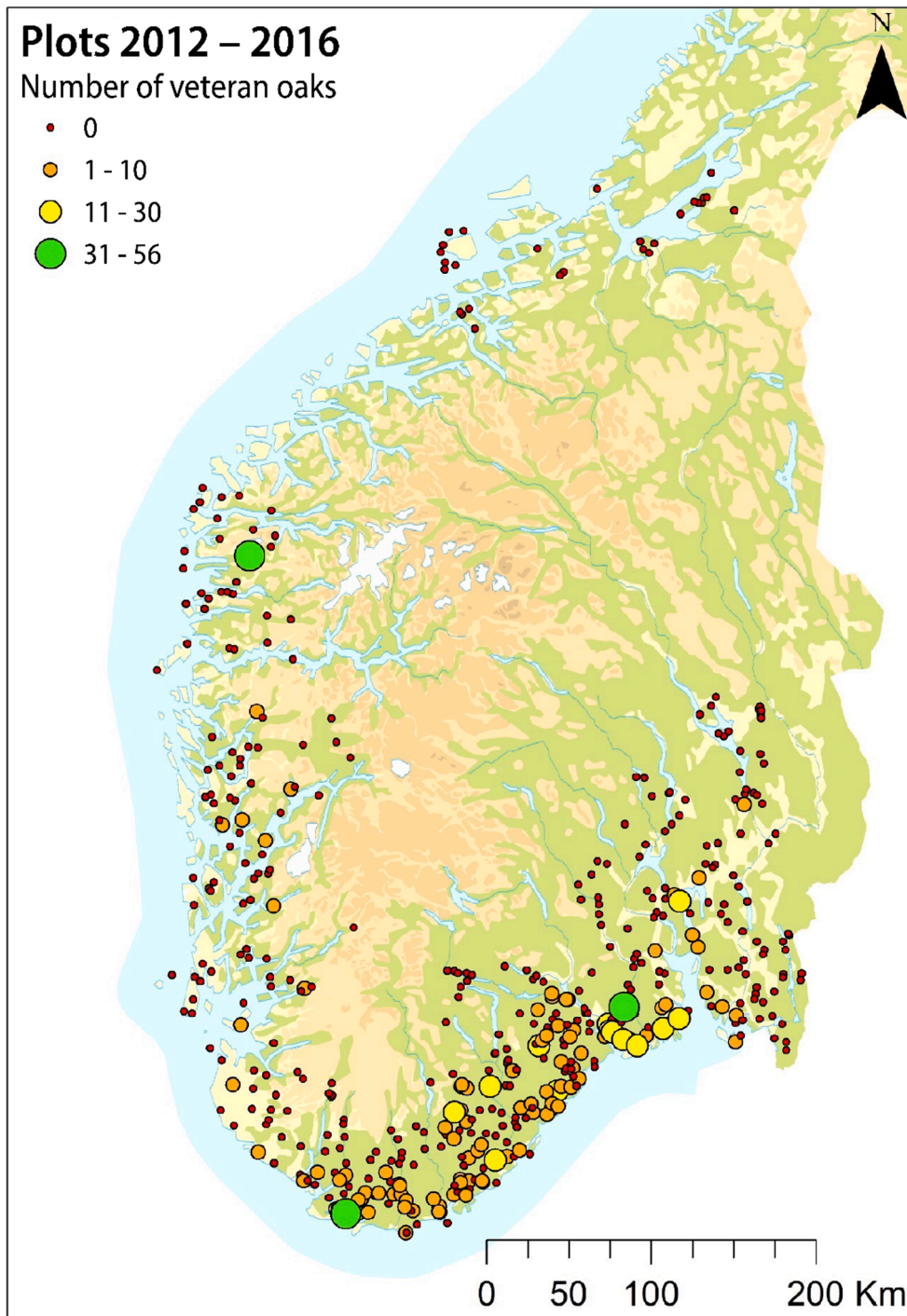


Fig. 2. Veteran oaks (see Box 1 for definition) registered during the baseline survey of 500 plots within the distribution area (Fig. 1) of oak in Norway. Small, red circles denote plots without veteran oaks, orange circles denote plots with 1–10 veteran oaks, yellow circles denote plots with 11–30 veteran oaks, and large, green circles denote plots with 31–56 veteran oaks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

estimated to occur in all of Norway in 2016 (Table 1). Approximately 60 500 veteran oaks (with a 95% confidence interval of 34 000 – 98 000) were covered by the special protection from the Norwegian Biodiversity Act (see Box 1), and an additional 2 300 veteran oaks (230 – 6 000) were occurring in nature reserves not covered by the Act. However, around 54% of the estimated total number of veteran oaks (74 700 oaks with a 95% confidence interval of 31 770 – 138 000) were most likely occurring in areas where they did not receive special protection, i.e., more than 20 m within productive forest.

A total of 25 670 “top quality” veteran oaks were estimated to occur in all of Norway in from the baseline survey (Table 1), of which 4540 were likely to occur either in nature reserves (2% of the 4540 trees) or in areas covered by the Norwegian Biodiversity Act (the remaining 98%). Thus, around 82% of the “top quality” veteran oaks estimated to occur in Norway were not covered by legislation providing special protection.

### 3.2. Mortality trend

Based on numbers adjusted from the revisit, 130 500 veteran oaks were estimated to occur in all of Norway in 2019 (Table 1), i.e., we estimated a total loss of 7 600 veteran trees (Table 1). Thus, approximately 5.5% of the veteran oaks were estimated to be lost during between the baseline survey and the revisit. The estimated mean annual decline depended on the number of years this was calculated over; assuming all lost trees got lost after the first year of the baseline survey (2012) yielded an annual decline of 0.80, however, assuming all trees got lost after the first baseline finished (2016) resulted in an annual decline of 1.86. Using a mean of five years, the annual decline was estimated to 1.18.

Of the 62 800 veteran oaks covered by the Norwegian Biodiversity Act or occurring in nature reserves, we estimated a loss of 3 850 trees between the baseline survey and the revisit (with a 95% confidence interval of 660 – 8800; Table 1). For “top quality” veteran oaks, we estimated a loss of 4.3% oaks between 2016 and 2019 (Table 1).

### 3.3. Recruitment potential

Small oaks occurred in 203 of the 500 monitored plots, while medium oaks occurred in 148 of the plots. Recruitment oaks were present in most plots with veteran oaks (Fig. 3A). Only three of the 114 plots with veteran oaks were lacking any recruitment oaks, while nine of the plots with veteran oaks had no medium sized recruitment oaks. Plots

**Table 1**

Estimated total numbers (with 95% confidence interval) of veteran oaks and the subset “top quality” veteran oaks occurring in all of Norway after the baseline survey (2012–2016) and after the first revisit (2019), including estimated number and proportion of veteran oaks protected by legislation (either occurring in nature reserves or being covered by the Norwegian Biodiversity Act, see Box 1) and estimated number and proportion of veteran oaks lost between the first monitoring period and the revisit.

Oak category	Baseline survey (2012–2016)	First monitoring revisit (2019)		
	Total	Total	Lost since 2016 †	% lost
Veteran oaks	138 000 (70 160–226 170)	130 500 (66 600–212 900)	7 600 (3 100–13 900)	5.5
Veteran oaks protected by legislation*	62 800 (34 230–104 000)	58 950 (33 570–95 200)	3 850 (660–8 800)	6.1
“Top quality” veteran oaks <sup>‡</sup>	25 670 (4 310–62 300)	24 370 (3 560–60 340)	1 100 (33–2 600)	4.3

^ Subset of all veteran oaks. \* Within protected area or covered by special protection as a ‘selected habitat type’, see Box 1. † More precisely, lost in the three to seven year-interval between the baseline survey (2012 – 2016) and the revisit (2019).

without veteran oaks rarely had any recruitment oaks, and none of these plots had 50 or more medium oaks (Fig. 3B).

### 3.4. Ecological state variables

Average circumference ( $\pm$ standard deviation) at breast height of the veteran oaks was 207 cm ( $\pm$ 85 cm), and 63% of the veteran oaks were visibly hollow. The 95 “top quality” veteran oaks registered had an average circumference of 293 cm ( $\pm$ 132 cm) and 79% were visibly hollow.

Of the 657 veteran oaks registered in the baseline survey, 78.5% were surrounded by trees of approximately the same height as the oak. Although 417 of the oaks occurred within forest (including the 20 m edge zone, Box 1), 165 of the 240 oaks occurring outside forest were also surrounded by regrowth in the form of trees the same height as the oak. Vitality and surrounding regrowth were reassessed for the 600 veteran oaks that were found during the revisit. No change was reported for the majority of the oaks (460 oaks with no change in vitality, 426 oaks with no change in regrowth). Thirty-two oaks (5.4%) had a reported higher vitality at the revisit compared with the initial assessment, while 105 oaks (17.6%) had declined in vitality since the baseline survey. The degree of regrowth around the veteran oak had increased for 53 oaks (8.9%) between the baseline survey and the revisit, whilst for 117 oaks (19.6%) the regrowth by shrubs and trees was less at the revisit in 2019 relative to the baseline survey. These differences in regrowth were not clearly linked to legal protection of the tree, as veteran oaks covered by protective legislation constituted 52% of the trees surrounded by less regrowth at the revisit, and 57% of the trees surrounded by more regrowth.

### 3.5. Monitoring program design

Estimates of precision and detectable change based on resampling of the dataset from the baseline survey showed that increasing the number of plots above 500 had little effect, with even doubling of the number of plots (1000) resulting in only marginal changes in precision of estimates and the ability to detect change (Fig. 4). The current monitoring program should be able to detect 5% changes in number of veteran oaks in Norway, and indeed, the revisit led to detection of a reduction of 5.5% in total number of veteran oaks.

## 4. Discussion

By systematically surveying veteran oaks within the entire distribution zone for oak in Norway, we were able to estimate the total number of veteran oaks in Norway to approximately 138 000 trees. This far exceeds the 10 615 veteran oaks currently registered in the national database (Naturbase, accessed 18.02.22), and clearly demonstrates the need for continued surveying to improve the foundation for a knowledge-based land management. The Norwegian Biodiversity Act requires that e.g. land owners and municipalities seek to avoid measures that harm veteran oaks (outside productive forest, see Box 1), and knowledge of the occurrence of veteran oaks at the planning stage is vital to achieve this efficiently. Many of our results and conclusions may have relevance also for veteran trees of other species than oak.

### 4.1. Veteran tree mortality

Human safety and land development are common causes for intentional removal of large, old trees reported also from other countries, and in some countries selective harvesting of large trees contributes to their mortality (Lindenmayer et al., 2014). In urban areas and close to roads, the attributes of veteran trees contributing to high biodiversity value often correlate with high perceived risk for human safety, such as dead branches in the canopy and formation of trunk cavities (Carpaneto et al., 2010). Dead branches have been found to promote species richness of

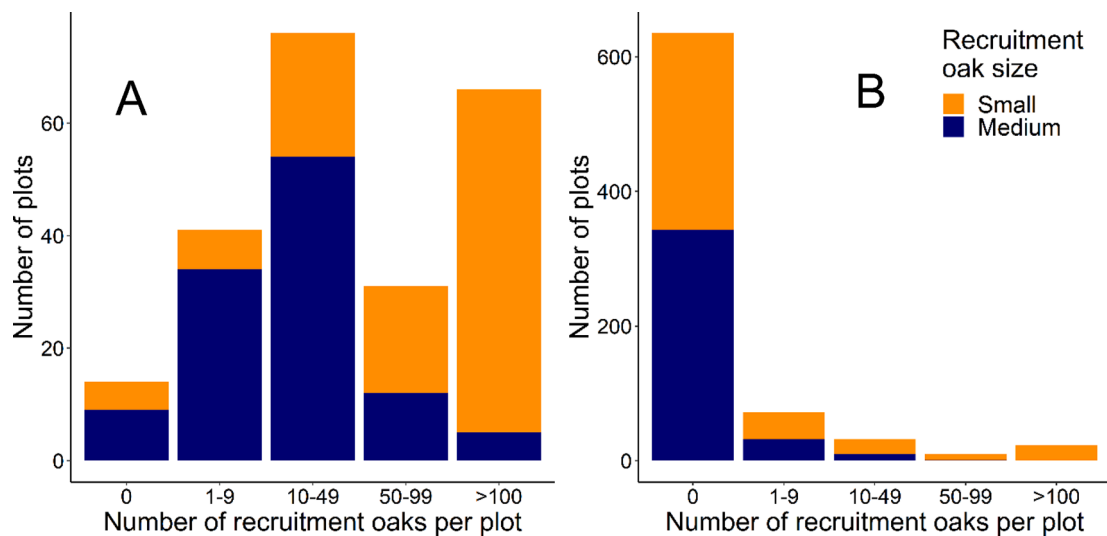


Fig. 3. Number of plots (A) with or (B) without veteran oaks present, where 0, 1–9, 10–49, 50–99 or > 100 small (dbh 10 - <40 cm, orange colour) or medium (dbh 40 - <63 cm, blue colour) recruitment oaks. Note that since both small and medium recruitment oaks can be present at the same plot, the summed number of plots can be higher than 500. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

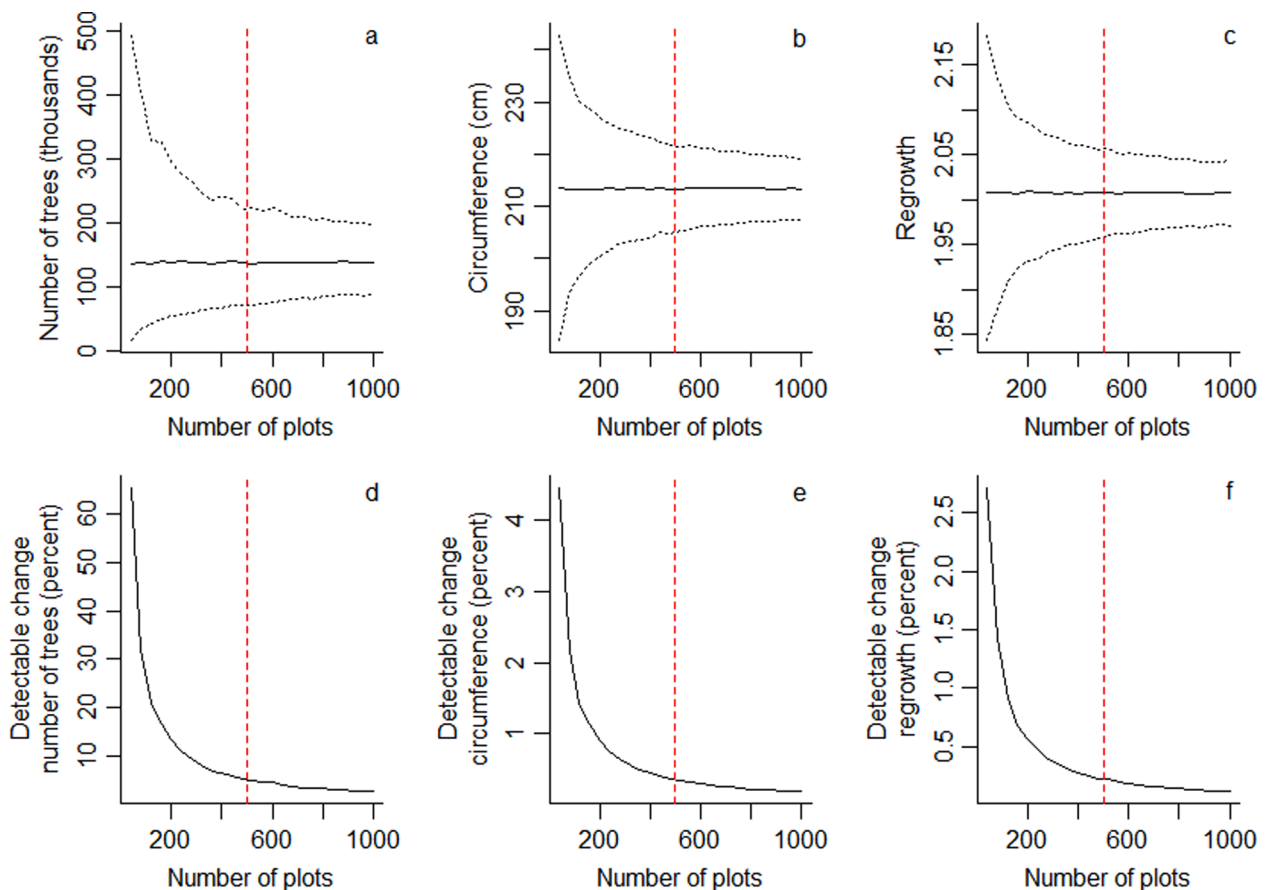


Fig. 4. Precision of total estimates (a – c) and detectable change (d – f) for variables such as total number of veteran oak trees, average circumference at breast height and regrowth as a function of number of plots monitored. The red dashed line marks the number of plots (500) in the current monitoring program. In the graphs for precision (a – c), the unbroken line marks the average estimate, while the dotted, black lines denote 95% confidence intervals (based on bootstrapping,  $n = 2000$ ). The graphs for detectable change assume 80% power and a significance threshold of 0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lichens (Lie et al., 2009) and red-listed beetles (Pilskog et al., 2016), while cavities host rare and specialized species of invertebrates (Müller et al., 2014, Taylor and Ranius 2014, Pilskog et al., 2020). Furthermore,

in Norway, the main distribution area for oak along the south-eastern coast is also the part of the country with highest population density and thus pressure on land development. Thus, the loss reported in the

present study of 5.5% of the veteran oaks within three to seven years was not wholly unexpected, also considering previous indications of a decline for veteran oaks in Norway (Sverdrup-Thygeson et al., 2014).

The revisit did not register recruitment into the category of veteran oak at the monitoring plots. Some forest inventories find increasing numbers of large trees over the last 40 to 90 years (Faison 2014, Henttonen et al., 2019). Recruitment of veteran oaks in Norway would occur through two processes; 1) by the development of hollows, with an opening diameter of > 5 cm and where the interior of the hollow is larger than the opening (cf. Box 1, page 7), or 2) by a diameter increase of at best > 1 cm (for trees just below the size limit at the baseline survey; the medium size class includes trees from 40 - <63 cm dbh). Due to the slow process of oak growth and cavity formation (Ranius et al., 2009a), we believe that the short timespan in our study makes recruitment unlikely. Nevertheless, with the lack of recruitment data, we might overestimate net decline, and future monitoring should include data collection also on recruitment oaks. On the other side, all veteran oaks from the baseline survey were registered into national open access databases (see further discussion below). We consider it likely that trees recorded in national databases have lower probability of being logged than trees not “publicly known”. Thus, the requirement of publicizing locations of monitoring trees could potentially contribute to an underestimate of net decline.

The estimated annual mortality rate of about 1% for veteran oaks in Norway is in line with trends reported from other studies of large, old trees (Cannon et al., 2022). For instance, Drobyshev et al. (2008) calculated an average mortality rate of 1.1% for oaks older than 200 years in Sweden, while Richardson et al. (2009) reported mortality rates for large trees in New Zealand ranging from 0.2% to 2.2% depending on species. Van Mantgem et al. (2009) estimated mortality rates for trees in unmanaged, old forests in the western United States, based on empirical data spanning the period between 1955 and 2007. They found a dramatic increase in annual mortality for all tree species, size and age classes, on average increasing from approximately 0.25% prior to 1960, to around 1.25% after 2000. Due to the uniform increase in mortality across tree size and age, and the lack of increase in forest density which could imply increased competition, Van Mantgem et al. (2009) suggest that the cause could be regional warming and resulting increase in water deficits.

In Norway, the increase in precipitation following global warming makes increasing mortality due to a general increase in water deficits less likely, but factors such as disease (e.g., sudden oak death, *Phytophthora ramorum*, Grünwald et al., 2019), pollution and increased nitrogen deposition, complex effects of climate change, cessation of traditional management or habitat fragmentation (Lindenmayer et al., 2014) could potentially increase mortality of large, old trees. We currently lack data on mortality rates of recruitment oaks and thus are not able to assess if mortality is uniform across size classes. Thus, we do not know the main driving factors behind veteran oak mortality in Norway. We note, however, that at least 44% of the mortality of veteran oaks documented during the revisit was due to intentional removal.

#### 4.2. Access to tree locations may influence fates of monitored trees

The Norwegian veteran oak monitoring program contributes substantially to the knowledge of veteran oak occurrences, as all registered veteran oaks are reported with coordinates to national databases with open access. While this increases the utility of the monitoring for nature management, it can also reduce the representativity of data from revisits, as registered veteran oaks might for instance be less likely to be cut down than unregistered veteran oaks. It is recommended not to reveal locations of monitoring points if surveys are repeated at the same locations over time (Boutin et al., 2009), but as the Norwegian oak monitoring program is funded by environmental authorities, the legal obligation to provide relevant environmental information to all stakeholders was considered more important than ensuring continued

representativity of monitoring data. The dataset will, however, be useful for assessing the value of legislative measures to protect veteran oaks, for instance by comparing trends for oaks encompassed by the Norwegian Biodiversity Act (Lovdata 2011) or occurring in nature reserves, with unprotected oaks occurring in productive forests.

#### 4.3. Limitations of current legislation

Only about 2 300 veteran oaks in Norway were estimated to occur in nature reserves, but approximately 44% were occurring in areas where the special protection from the Norwegian Biodiversity Act applied. However, 54% of veteran oaks were estimated to occur in areas without special protection, i.e., within productive forest. Although Norwegian forestry practice includes environmental considerations, mainly through the PEFC standard (Program for the Endorsement of Forest Certification), these measures do not target veteran oaks specifically. The measures include prioritization of deciduous trees such as oak for retention trees on clear-cuts, and registration of occurrences of oaks with dbh > 50 cm and hollow oaks with dbh > 30 cm for potential protection as a point-based woodland key habitat. The revisit of the veteran oaks registered during the baseline survey did not indicate a higher mortality in productive forest. When only considering veteran oaks that had clearly died due to human activities, 60% of these actually occurred within nature reserves or areas covered by the Norwegian Biodiversity Act, i.e. the mortality rate of protected trees was considerably higher (6.1%; Table 1) than of trees in productive forests (5.0%). The majority of protected veteran trees (80%) had been considered vital (i.e. alive and without dead branches) in the initial survey, i.e. removal for human safety seems not to be a plausible cause, although in a couple of cases the trees occurred close to roads and might have been felled as a traffic safety measure. Several of the areas seemed, however, to have been converted to construction sites or quarries. These examples illustrate cases where the special protection intended for biodiversity hotspots such as veteran oaks, through the Norwegian Biodiversity Act, is set aside to prioritize other societal concerns. This is not forbidden through the Act but making such allowances too frequently will drastically weaken the protection of veteran oaks in Norway.

#### 4.4. Can recruitment counteract the decline?

Whether an annual mortality rate of 1–1.5% results in a net decline of veteran oaks in Norway, depends on rate of recruitment. Gibbons et al. (2008) estimated that scattered, mature trees in agricultural landscapes in Spain, the US, Australia and Costa Rico would disappear in 90–180 years, due to exceedance mortality over recruitment. We do not yet have estimates for rate of recruitment of veteran oaks in Norway, as recruitment was not registered during the revisit, both due to practical concerns and the relatively short time since the baseline survey, but recruitment will be an important variable to assess in future revisits. However, we found that small and medium recruitment oaks occurred at almost every plot with one or more veteran oaks. Thus, there seems to be potential for adequate recruitment, but we do not know the mortality rate for such recruitment trees, nor the time required for a medium oak (dbh 40–62 cm) to develop into a veteran oak (dbh > 62 cm, or visible hollow and dbh > 30 cm). Drobyshev et al. (2008) modelled, based on empirical data from Sweden, that with a regular annual mortality of 1%, long-term maintenance of 20 trees older than 200 years per hectare (ha) would require input of one to five trees per ha each year into the 100–150 year old class. Assuming that trees older than 200 years would be considered veteran trees by our definition, a density of 20 trees per ha seems unrealistic for Norwegian conditions, as that would equal 500 veteran trees per monitoring plot. The highest density of veteran oaks registered in our study was 56 in one plot, i.e., approximately two per ha. Assuming that medium oaks in our study are comparable to the 100–150 year old trees in Drobyshev et al. (2008), the presence of at least one medium oak and often more than ten at the majority of plots



with veteran oaks, might be sufficient to maintain current densities of veteran oaks in Norway. However, the majority of plots without veteran oaks did not have any recruitment oaks at all, and so the potential for increasing the distribution and population size of veteran oaks in Norway seems weaker. The high number of threatened species associated with veteran oaks in Norway (Tingstad et al., 2018) indicates that the current population size is insufficient for biodiversity conservation, and there might even still be an extinction debt in parts of the country stemming from past intensive oak logging (Pilskog et al., 2018).

#### 4.5. The need for improved protection of veteran trees

The estimated loss of 7600 veteran oaks in Norway over three to seven years, indicated by the present study, calls for improved protection and management of this biodiversity hotspot. The high proportion of trees lost from areas covered by the Norwegian Biodiversity Act indicates that the protection offered by this law should be applied more strictly in land management processes. The Act requires local authorities and landowners to seek to avoid negative effects on veteran oaks (The Norwegian Biodiversity Act §53). However, the efficiency of the Act in protecting veteran oaks depends on the prioritization of different societal concerns, as it does not forbid measures with negative effect on veteran oaks, and it depends on local authorities and landowners being aware of their responsibility in managing occurrences of veteran oaks on their property. Managing veteran oaks could also include positive measures, such as removing encroaching vegetation, although this is not required from landowners through the Act. Even the veteran oaks occurring outside forest were found during the monitoring to frequently be surrounded by regrowth in the form of trees as tall as the oaks themselves. For oaks previously growing in open, sunny conditions, such regrowth can result in a decline in oak vitality and negative effects on associated species adapted to sun-exposed conditions (Ranius and Jansson 2000, Gough et al., 2014). Other measures that can prolong oak vitality include crown management for stabilization, which can also reduce risk to human safety from veteran trees in traffic and urban areas. Local authorities and landowners should be informed both of their responsibility to avoid damaging veteran oaks, and of such positive management measures. Furthermore, though not required by the Norwegian Biodiversity Act at present, local authorities and landowners should be involved in management plans to ensure adequate recruitment of veteran oaks on a long-term basis.

#### 4.6. Plans for further monitoring of veteran oaks

Planning for adequate recruitment of veteran oaks on a national basis requires follow-up of the Norwegian veteran oak monitoring program presented in this study, with a revisit of plots including registration of recruitment as well as mortality of recruitment trees. Plots with veteran oaks could be prioritized to lower costs, but ideally all 500 plots should be revisited for a thorough registration of recruitment. The frequency of revisits should be considered in light of both natural processes such as oak growth and cavity formation, but also local and global anthropogenic influences. Modelling showed that increasing the number of plots had little effect on precision of estimates and detectable change, hence, increasing sample size should be of less importance compared to sampling recruitment into the veteran oak category.

As old, veteran oaks are hotspots for a rich biodiversity, future monitoring should also include the associated species communities. Monitoring of insects in veteran oaks has been suggested and partly tested (Hatlevoll et al., 2019, Burner et al., 2021), and should be coordinated with the National insect monitoring in Norway (Åström et al., 2020).

#### 4.7. The role of veteran trees in a climate change mitigation perspective

While oak in Norway is at the northernmost border of its distribution

in Europe, the ongoing climate change might shift oak distribution northward (Dyderski et al., 2018, Axer et al., 2021), thereby increasing the importance of populations of oak and associated species in Norway. Veteran oaks and other very old trees can be especially important in light of climate change, as they represent an evolutionary resource with genotypes stemming from establishment under a range of different environmental conditions (Cannon et al., 2022). Veteran trees of old age can bridge the gap between occurrences of rare environmental extremes, providing new individuals with genes that have not been selected for in many decades or even centuries (Cannon et al., 2022). Thus, safeguarding veteran trees and their long-term survival might increase climate resilience, as well as prevent biodiversity loss and maintain vital ecosystem functions.

#### 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.

#### Data availability

Data will be made available on request.

#### Acknowledgements

We thank David Arnott, Ryan Burner, Toril Hasle, Kristina Hatlevoll, Lisa Fagerli Lunde, Adrian Rasmussen, Markus Sydenham, Ronny Steen, Simen Sverdrup-Thygeson and Ross Wetherbee, for contributing to collecting data in the field. Two anonymous referees provided valuable comments to a previous version of this manuscript.

Funding: This work was supported by the Norwegian Environment Agency (project "Overvåking hule eiker", contract no. 19047020).

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120624>.

#### References

- Ahlström, A.P., Bjørkelo, K., Fadnes, K., 2019. AR5 Klassifikasjonssystem. Klassifisering av arealressurser. NIBIO Bok 5 (5).
- Andersson, R., Östlund, L., 2004. Spatial patterns, density changes and implications on biodiversity for old trees in the boreal landscape of northern Sweden. *Biol. Conserv.* 118, 443–453. <https://doi.org/10.1016/j.biocon.2003.09.020>.
- Åström, J., Birkemoe, T., Dahle, S., Davey, M., Ekrem, T., Endrestøl, A., Fossøy, F., Nystad Handberg, Ø., Hanssen, O., Magnussen, K., Majaneva, M.A.M., Navrud, S., Staverløkk, A., Sverdrup-Thygeson, A., Ødegaard, F., 2020. Proposal for a national insect monitoring program in Norway – Findings from a pilot study with cost-benefit analysis. NINA Report 1725. 107 p. (in Norwegian, English abstract) <https://brage.nina.no/nina-xmlui/handle/11250/2646943>.
- Axer, M., Schlicht, R., Kronenberg, R., Wagner, S., 2021. The potential for future shifts in tree species distribution provided by dispersal and ecological niches: a comparison between beech and oak in Europe. *Sustain.* 13, 13067. <https://doi.org/10.3390/su132313067>.
- Bates, J.W., Brown, D.H., 1981. Epiphyte differentiation between *Quercus petraea* and *Fraxinus excelsior* trees in a maritime area of South West England. *Vegetatio* 48, 61–70. <https://doi.org/10.1007/bf00117362>.
- Blicharska, M., Mikusiński, G., 2014. Incorporating social and cultural significance of large old trees in conservation policy. *Conserv. Biol.* 28, 1558–1567.
- Boutin, S., Haughland, D.L., Schieck, J., Herbers, J., Bayne, E., 2009. A new approach to forest biodiversity monitoring in Canada. *For. Ecol. Manag.* 258 <https://doi.org/10.1016/j.foreco.2009.08.024>. S168–S175.
- Burner, R.C., Sverdrup-Thygeson, A., Birkemoe, T., 2021. National oak monitoring: testing traps and sampling strategies. MINA fagrapport 70, 29 p in Norwegian, English abstract.
- Cannon, C.H., Piovesan, G., Munné-Bosch, S., 2022. Old and ancient trees are life history lottery winners and vital evolutionary resources for long-term adaptive capacity. *Nature Plants* 8, 136–145. <https://doi.org/10.1038/s41477-021-01088-5>.
- Carpaneto, G.M., Mazziotta, A., Coletti, G., Luiselli, L., Audisio, P., 2010. Conflict between insect conservation and public safety: The case study of a saproxylic beetle

- (*Osmoderma eremita*) in urban parks. *J. Insect Conserv.* 14, 555–565. <https://doi.org/10.1007/s10841-010-9283-5>.
- Dixon, P.M., Ellison, A.M., Gotelli, N.J., 2005. Improving the precision of estimates of the frequency of rare events. *Ecology* 86, 1114–1123. <https://doi.org/10.1890/04-0601>.
- Drobyshev, I., Niklasson, M., Linderson, H., Sonesson, K., Karlsson, M., Nilsson, S.G., Lanner, J., 2008. Lifespan and mortality of old oaks—Combining empirical and modelling approaches to support their management in Southern Sweden. *Durée de vie et mortalité des vieux chênes: une approche empirique combinée à une modélisation pour un appui à leur gestion dans le sud de la Suède. Ann. For. Sci.* 65 (4).
- Drobyshev, I., Niklasson, M., 2010. How old are the largest southern Swedish oaks? A dendrochronological analysis. *Ecol. Bull.* 53, 155–164.
- Dyderski, M.K., Paž, S., Frelich, L.E., Jagodziński, A.M., 2018. How much does climate change threaten European forest tree species distributions? *Glob. Change Biol.* 24, 1150–1163. <https://doi.org/10.1111/gcb.13925>.
- Faison, E.K., 2014. Large old tree declines at broad scales: a more complicated story. *Conserv. Lett.* 7, 70–71. <https://doi.org/10.1111/conl.12075>.
- Gibbons, P., Lindenmayer, D.B., Fischer, J., Manning, A.D., Weinberg, A., Seddon, J., Ryan, P., Barrett, G., 2008. The future of scattered trees in agricultural landscapes. *Conserv. Biol.* 22, 1309–1319. <https://doi.org/10.1111/j.1523-1739.2008.00997.x>.
- Gilhen-Baker, M., Roviello, V., Beresford-Kroeger, D., Roviello, G.N., 2022. Old growth forests and large old trees as critical organisms connecting ecosystems and human health. A review. *Environ. Chem. Lett.* 20, 1529–1538. <https://doi.org/10.1007/s10311-021-01372-y>.
- Gough, L.A., Birkemoe, T., Sverdrup-Thygeson, A., 2014. Reactive forest management can also be proactive for wood-living beetles in hollow oak trees. *Biol. Conserv.* 180, 75–83. <https://doi.org/10.1016/j.biocon.2014.09.034>.
- Grünwald, N.J., LeBoldus, J.M., Hamelin, R.C., 2019. Ecology and evolution of the sudden oak death pathogen *Phytophthora ramorum*. *Ann. Rev. Phytopathol.* 57, 301–321. <https://doi.org/10.1146/annurev-phyto-082718-100117>.
- Hatlevoll, K., Burner, R., Ørka, H.O., Arnott, D., Lunde, L.D., Evju, M., Birkemoe, T., Sverdrup-Thygeson, A., 2019. National monitoring of hollow oaks: results from the first revisit. MINA fagrapport 62, 36 p in Norwegian, English abstract.
- Henttonen, H.M., Nöjd, P., Suvanto, S., Heikkinen, J., Mäkinen, H., 2019. Large trees have increased greatly in Finland during 1921–2013, but recent observations on old trees tell a different story. *Ecol. Ind.* 99, 118–129. <https://doi.org/10.1016/j.ecolind.2018.12.015>.
- IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. S. Díaz, et al. (eds.). IPBES secretariat, Bonn, Germany. 56 p.
- Jonsell, M., 2012. Old park trees as habitat for saproxylic beetle species. *Biodiv. Conserv.* 21, 619–642. <https://doi.org/10.1007/s10531-011-0203-0>.
- Jonsell, M., Weslien, J., Ehnstrom, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiv. Conserv.* 7, 749–764.
- Laurance, W.F., Delamónica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. *Nature* 404. <https://doi.org/10.1038/35009032>.
- Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D., Gibbons, P., 2014. The future of large old trees in urban landscapes. *PLOS ONE* 9, e99403.
- Lie, M.H., Arup, U., Grytnes, J.-A., Ohlson, M., 2009. The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. *Biodiv. Conserv.* 18, 3579. <https://doi.org/10.1007/s10531-009-9661-z>.
- Lindenmayer, D.B., Laurance, W.F., 2016. The unique challenges of conserving large old trees. *Trends Ecol. Evol.* 31, 416–418. <https://doi.org/10.1016/j.tree.2016.03.003>.
- Lindenmayer, D.B., Likens, G.E., 2010. The science and application of ecological monitoring. *Biol. Conserv.* 143, 1317–1328. <https://doi.org/10.1016/j.biocon.2010.02.013>.
- Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., Stein, J.A., 2014. New policies for old trees: Averting a global crisis in a keystone ecological structure. *Conserv. Lett.* 7, 61–69. <https://doi.org/10.1111/conl.12013>.
- Liu, J., Lindenmayer, D.B., Yang, W., Ren, Y., Campbell, M.J., Wu, C., Luo, Y., Zhong, L., Yu, M., 2019. Diversity and density patterns of large old trees in China. *Sci. Tot. Environ.* 655, 255–262. <https://doi.org/10.1016/j.scitotenv.2018.11.147>.
- Livesley, S.J., McPherson, E.G., Calfapietra, C., 2016. The urban forest and ecosystem services: Impacts on urban water, heat, and pollution cycles at the tree, street, and city scale. *J. Environ. Qual.* 45, 119–124. <https://doi.org/10.2134/jeq2015.11.0567>.
- Lovdata. 2011. Forskrift om utvalgte naturtyper etter naturmangfoldloven. <http://lovdata.no/dokument/SF/forskrift/2011-05-13-512>.
- Müller, J., Jarzabek-Müller, A., Bussler, H., Gossner, M.M., 2014. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Anim. Conserv.* 17, 154–162. <https://doi.org/10.1111/acv.12075>.
- Nolan, V., Reader, T., Gilbert, F., Atkinson, N., 2020. The Ancient Tree Inventory: A summary of the results of a 15 year citizen science project recording ancient, veteran and notable trees across the UK. *Biodiv. Conserv.* 29, 3103–3129. <https://doi.org/10.1007/s10531-020-02033-2>.
- Nordén, B., Jordal, J.B., Evju, M., 2018. Can large unmanaged trees replace ancient pollarded trees as habitats for lichenized fungi, non-lichenized fungi and bryophytes? *Biodiv. Conserv.* 27, 1095–1114. <https://doi.org/10.1007/s10531-017-1482-x>.
- Parmain, G., Bouget, C., 2018. Large solitary oaks as keystone structures for saproxylic beetles in European agricultural landscapes. *Insect Conserv. Divers.* 11, 100–115. <https://doi.org/10.1111/icad.12234>.
- Parra-Saldívar, A., Abades, S., Celis-Diez, J.L., Gelcich, S., 2020. Exploring perceived well-being from urban parks: Insights from a megacity in Latin America. *Sustain.* 12, 7586. <https://doi.org/10.3390/su12187586>.
- Pilskog, H.E., Birkemoe, T., Framstad, E., Sverdrup-Thygeson, A., 2016. Effect of habitat size, quality, and isolation on functional groups of beetles in hollow oaks. *J. Insect Sci.* 16, 26. <https://doi.org/10.1093/jisesa/iev145>.
- Pilskog, H.E., Sverdrup-Thygeson, A., Evju, M., Framstad, E., Birkemoe, T., 2018. Long-lasting effects of logging on beetles in hollow oaks. *Ecol. Evol.* 8, 10126–10137. <https://doi.org/10.1002/ece3.4486>.
- Pilskog, H.E., Birkemoe, T., Evju, M., Sverdrup-Thygeson, A., 2020. Species composition of beetles grouped by host association in hollow oaks reveals management-relevant patterns. *J. Insect Conserv.* 24, 65–86. <https://doi.org/10.1007/s10841-019-00210-5>.
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* 95, 85–94. [https://doi.org/10.1016/S0006-3207\(00\)00007-0](https://doi.org/10.1016/S0006-3207(00)00007-0).
- Ranius, T., Johansson, P., Berg, N., Niklasson, M., 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *J. Veg. Sci.* 19, 653–662. <https://doi.org/10.3170/2008-8-18433>.
- Ranius, T., Niklasson, M., Berg, N., 2009a. Development of tree hollows in pedunculate oak (*Quercus robur*). *For. Ecol. Manag.* 257, 303–310. <https://doi.org/10.1016/j.foreco.2008.09.007>.
- Ranius, T., Svensson, G.P., Berg, N., Niklasson, M., Larsson, M.C., 2009b. The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. *Ann. Zool. Fenn.* 46, 205–216. <https://doi.org/10.5735/086.046.0305>.
- Richardson, S.J., Smale, M.C., Hurst, J.M., Fitzgerald, N.B., Peltzer, D.A., Allen, R.B., Bellingham, P.J., McKelvey, P.J., 2009. Large-tree growth and mortality rates in forests of the central North Island. *New Zealand J. Ecol.* 33, 208–215.
- Skarpaas, O., Blumentrath, S., Evju, M., Sverdrup-Thygeson, A., 2017. Prediction of biodiversity hotspots in the Anthropocene: The case of veteran oaks. *Ecol. Evol.* 1–11. <https://doi.org/10.1002/ece3.3305>.
- Strand, G.-H., Verner Holst Bloch, V., 2009. Statistical grids for Norway. Documentation of national grids for analysis and visualisation of spatial data in Norway. (No. 9). Statistics Norway.
- Sundberg, S., Carlberg, T., Sandström, J., Thor, G. (eds.) 2019. The importance of vascular plants (notably woody species) to other organisms. *ArtDatabanken Rapportser*; 22. (In Swedish, English abstract) <https://www.artdatabanken.se/globalassets/ew/subw/artd/2-var-verksamhet/publikationer/vardvaxters-betydelse-for-andra-organismer-med-fokus-pa-verdattade-vardvaxter/vardartsrapport.pdf>.
- Svensson, A., Eriksen, R., Hysten, G., Granhus, A. 2021. The forest in Norway. Statistics of forest condition and forest resources in Norway for the period 2015–2019. NIBIO Report 7 (142). (In Norwegian, English abstract) [https://nibio.brage.unit.no/nibio-xmlui/bitstream/handle/11250/2763651/NIBIO\\_RAPPORT\\_2021\\_7\\_142.pdf?sequence=2&isAllowed=y](https://nibio.brage.unit.no/nibio-xmlui/bitstream/handle/11250/2763651/NIBIO_RAPPORT_2021_7_142.pdf?sequence=2&isAllowed=y).
- Sverdrup-Thygeson, A., Bratli, H., Brandrud, T. E., Endrestøl, A., Evju, M., Hanssen, O., Skarpaas, O., Stabbetorp, O., Ødegaard, F. 2011. Large, hollow oaks – a hotspot-habitat. Final report from the second period of the ARKO-project. NINA Report 710, 47 p. (In Norwegian, English abstract) <https://www.nina.no/archive/nina/pppbasepdf/rapport/2011/710.pdf>.
- Sverdrup-Thygeson, A., Evju, M., Skarpaas, O. 2013. National monitoring of hollow oaks in Norway. Description of a monitoring method developed in the ARKO project. NINA Report 1007, 29 p. (In Norwegian, English abstract) <https://www.nina.no/archive/nina/PppBasePdf/rapport/2013/1007.pdf>.
- Sverdrup-Thygeson, A., Rasmussen, A., Hanssen, O., Evju, M. 2014. Revisitation of hollow oaks surveyed 30 years ago. *INA Fagrapport* 23, 30 p. (In Norwegian, English abstract) <http://www.umb.no/statistik/ina/publikasjoner/fagrapport/ifa23.pdf>.
- Sverdrup-Thygeson, A., Evju, M., Skarpaas, O., Jacobsen, M., R., Birkemoe, T., 2018. National monitoring of hollow oaks. Results of baseline survey and proposed continuation. MINA Fagrapport 50 (In Norwegian, English abstract), p. 33.
- Taylor, A.R., Ranius, T., 2014. Tree hollows harbour a specialised oribatid mite fauna. *J. Insect Conserv.* 18, 39–55. <https://doi.org/10.1007/s10841-014-9613-0>.
- Tingstad, L., Grytnes, J.A., Felde, V.A., Juslén, A., Hyvärinen, E., Dahlberg, A., 2018. The potential to use documentation in national Red Lists to characterize red-listed forest species in Fennoscandia and to guide conservation. *Glob. Ecol. Conserv.* 15, e00410.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the Western United States. *Science* 323, 521–524. <https://doi.org/10.1126/science.1165000>.
- Wetherbee, R., Birkemoe, T., Skarpaas, O., Sverdrup-Thygeson, A., 2020. Hollow oaks and beetle functional diversity: Significance of surroundings extends beyond taxonomy. *Ecol. Evol.* 10, 819–831. <https://doi.org/10.1002/ece3.5940>.
- Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. *Trends Ecol. Evol.* 16, 446–453. [https://doi.org/10.1016/s0169-5347\(01\)02205-4](https://doi.org/10.1016/s0169-5347(01)02205-4).