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RESEARCH

# Ecological quality and structural diversity of Western Taiga habitat (*9010) in Estonia's Natura 2000 network

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**Abstract** Western Taiga habitat (*9010) plays the key role in the Natura 2000 network in Estonia. Natura 2000 is a European Union nature conservation area network aimed to safeguard the long-term survival of Europe's unique flora and fauna. This study examines the Western Taiga habitat within mixed oligo-mesotrophic and mesotrophic forests on mineral soils with a minimum age of 70 years, providing a comprehensive assessment of the habitat's current condition. The assessment includes ecological quality variables such as species composition, dead trees, lying deadwood, large trees, gaps, and characteristic species groups (mosses, vascular plants, lichens, fungi, beetles), as well as overall forest stand structural heterogeneity. The findings characterize the habitat's ecological quality at a specific point in time, offer practical guidelines for potential habitat quality improvements, and support conservation efforts within Estonia's Natura 2000 network.

**Keywords** Structural heterogeneity · Species composition · Characteristic species · Deadwood flow · Gaps

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## Introduction

Forests, as the dominant terrestrial ecosystems on Earth (Pan et al., 2013), support a substantial share of the terrestrial biodiversity (Maguire et al., 2007) with structural heterogeneity playing a crucial role in maintaining forest biodiversity (Thorn et al., 2017). While boreal and hemiboreal forests may seem less vulnerable globally due to relatively stable forest cover, many of these ecosystems have nonetheless suffered significant declines in ecological integrity (Halme et al., 2013). Forest landscapes that are unable to support the full array of ecosystem functions are often the result of even-aged management practices (Maguire et al., 2007). Balancing natural ecosystem dynamics with economic objectives, particularly those driven by even-aged management, remains a considerable challenge (Kuuluvainen et al., 2021), especially in the light of growing demand for biomass (Angelstam et al., 2020).

In response to the Convention on Biological Diversity (1992), there is an urgent need to restore the ecological quality of forest ecosystems. Several policy instruments have been introduced and implemented across Europe to protect, conserve, and restore forests. For instance, the European Green Deal (2023) aims to restore degraded ecosystems, facilitating the long-term recovery of resilient, biodiverse nature within the European Union (EU). The European Green Deal is grounded in multiple EU strategies, including Biodiversity Strategy for 2030 (2020), which seeks to halt biodiversity loss and restore ecosystems, fostering a more sustainable relationship between nature and society. The European Biodiversity Strategy aims to increase protected land areas, stating that at least 30% of European land should be protected by 2030, with 10% under strict protection. This includes all remaining primary and old-growth forests, highlighting the importance of conservation efforts to halt biodiversity loss. In Estonia, approximately 30% of forests are already protected, with around 17% under strict protection (Estonian Environmental Agency, 2023). However, protection alone does not always ensure favourable conservation status. Achieving the targets of the Biodiversity Strategy is closely tied to the role of Natura 2000 areas, a network of conservation areas established to ensure the long-term survival of Europe's most valuable and threatened species and habitats, as outlined in the EU Habitats Directive (92/43/EEC).

Natura 2000 forest habitat assessment in Estonia follows a classification system that groups habitats into representative classes (A, B, C) based on their conservation status (Palo et al., 2011). Class A includes well-preserved, near-natural forests with high structural complexity, which indicators include abundant deadwood, diverse tree age structures, and minimal past human impact. Class B represents semi-natural forests that retain key ecological features but show some signs of historical management or human disturbance. Class C consists of previously managed forests where natural characteristics have been partially lost, while the restoration potential remains.

Western Taiga habitats in Estonia, designated as Natura 2000 forest habitats, represent a unique ecological region, shaped by centuries of natural processes and anthropogenic activities (Palo, 2018). Historically, these habitats consisted of old-growth forests with minimal human disturbance. Nowadays, only a few remnants of such forests remain, primarily in Eastern Estonian regions (Paal, 2007). Although influenced by moderate forest management, these areas have developed towards more natural conditions. However, the need to balance conservation with economic interests may threaten the long-term sustainability of Western Taiga habitat and lead to a degradation of habitat's ecological values.

The ecological scope of different habitat types within the Natura 2000 network varies considerably. The Western Taiga habitat (*9010) plays a particularly important role in Estonia, where 37.7% of Natura 2000 protected forest habitats belong to this category (EELIS, 2024). The Western Taiga habitat encompasses a wide range of forest types (Paal, 2007) and spans large geographic areas across multiple countries (Paal, 2002). It includes old natural forests with key old-growth features, such as canopy gaps, groups of standing dead and downed trees, nursery logs, variable age structures, and natural disturbance areas with partially remaining deadwood. These stands consist of trees at various developmental stages, including those in early successional phases following disturbances (Palo, 2018). The habitat type represents forests growing on various soil types, including mesotrophic forests on mineral soils.

The objective of current research is to assess the Western Taiga habitats in Estonia at a specific point in time, focusing on their conservation status as classified by Natura 2000 representative classes (A, B, and C). The study examines how specific structural elements, such as canopy gaps and species spatial patterns, contribute to the overall habitat conservation status. The study aims to provide a comprehensive quantitative assessment of key structural features, addressing the lack of reference values for the habitats and supporting more informed conservation and restoration efforts. Understanding the structural diversity of Western Taiga habitats is important to achieving the conservation objectives outlined in the EU Biodiversity Strategy. With only around 15% of Natura 2000 habitats classified as being in favourable condition (European Commission, 2020), targeted conservation efforts are essential to restore and maintain these valuable ecosystems. The study provides important insights that can inform both policy and management practices aimed at improving the ecological integrity of these habitats in Estonia and across Europe.

## Materials and methods

### Sample plot inventory

The study is based on 100 circular sample plots that belong to the Estonian Network of Forest Research Plots (Kiviste et al., 2015) located in Eastern Estonia (Fig. 1). Ten different study areas were initially chosen, and within each area, 10 sample plots representing different Natura 2000 representative classes (A, B and C) were established. The sample plots originated from different Natura 2000 sites. The average size of the study areas is 23.9 ha (sd ± 26.1), and the average distance between study plots within the same area is 185.3 m (sd ± 93.0). The average distance between the 10 sample plots within each study area was calculated using QGIS 3.34.5's distance matrix tool. Pairwise distances between plot centres were computed and then averaged for each area to assess spatial distribution. Suitable Western Taiga habitats for plot establishment were selected from the EELIS (2014) map layers prior to the fieldwork. All sites are part of the Estonian Forest Conservation Area Network and represent different protection zones (Appendix 1; Natura assessment from EELIS).

The sample plots were selected from mixed oligo-mesotrophic and mesotrophic forests on mineral soils, with a minimum age of 70 years. Site types included *Oxalis*, *Oxalis-Myrtillus*, and *Oxalis-Vaccinium*, as classified by Lõhmus (2004). The sample plots represent forest types on Podzols and Gleysols (WRB, 2006), which are prevalent in Eastern Estonia. In contrast, habitats of type *9010 in the northern and western regions of Estonia are characterized by Leptosols and Regosols (WRB, 2006).

The sample plots were divided into three Natura representative classes (A, B, C) as determined by the Natura assessment based on the EELIS (2014) database. On each sample plot, the spatial positioning of the trees (alive, dead, and snags) was recorded explicitly and additional information about tree species, diameter

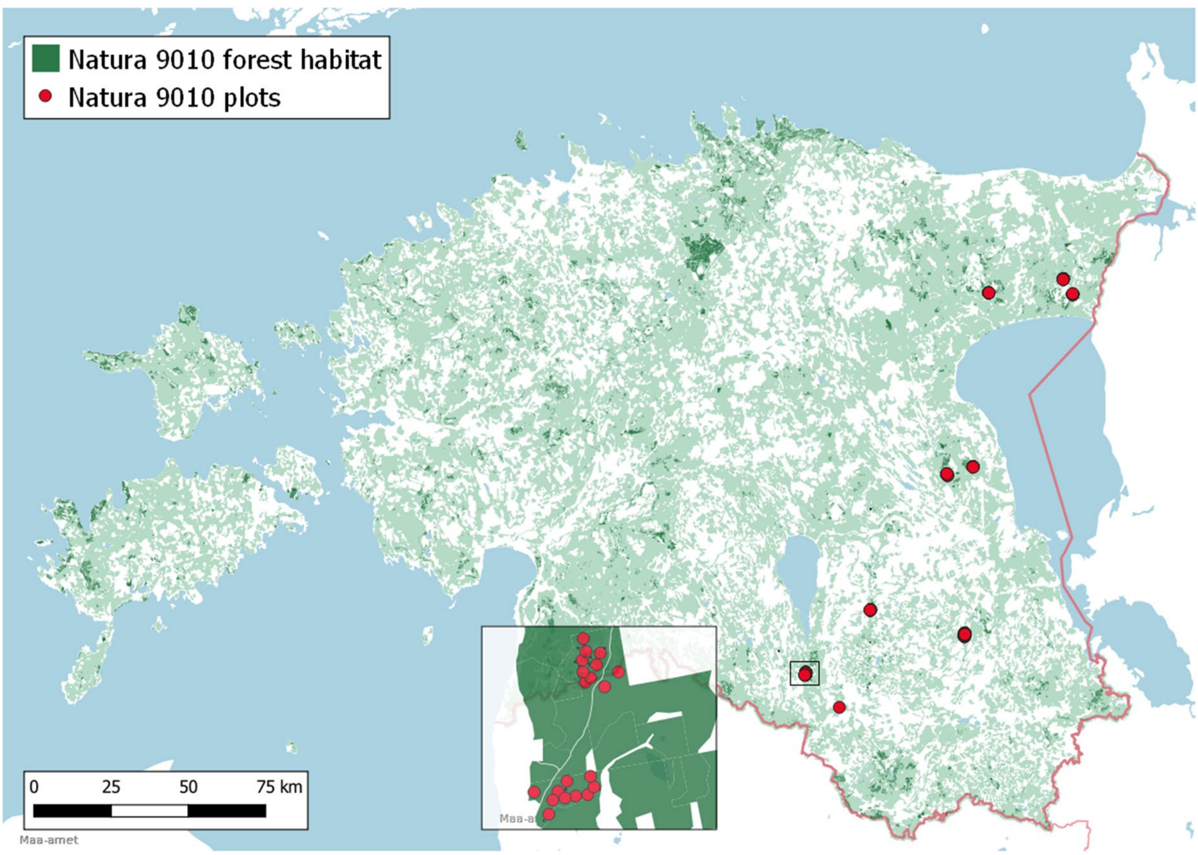


**Fig. 1** Position of sample plots in Estonia. One point represents several sample plots located close to each other. Light green represents forest cover

at breast height (dbh ≥ 4 cm), and the height of approximately every fifth living tree was gathered. The plot radius varied between 15 and 20 m depending on stand density and other stand characteristics. The location, decay stages (Table 1), and species of lying deadwood (diameter ≥ 10 cm at the coarser end) were also assessed.

The sample plots were dominated by Scots pine (*Pinus sylvestris*; 60%) and Norway spruce (*Picea abies*; 27%), with less representation of common aspen (*Populus tremula*; 8%) and birch (*Betula* spp., 5%) (Appendix 1). The dominant tree layer included species such as Norway spruce, Scots pine, birch, common aspen, black alder (*Alnus glutinosa*), European ash (*Fraxinus excelsior*), and Norway maple (*Acer platanoides*) (Appendix 1; species composition). Grey alder (*Alnus incana*), small-leaved lime (*Tilia cordata*), willow (*Salix* spp.), Scots elm, and European white elm (*Ulmus glabra* and *U. laevis*) were present in the codominant layer. The understorey was predominantly composed of Norway spruce, which was present in all 100 sample plots. Other understorey species included common hazel (*Corylus avellana*), birch, maple, common oak (*Quercus robur*), lime, rowan (*Sorbus aucuparia*), alder buckthorn (*Frangula alnus*), and bird cherry (*Prunus padus*). The tree species of lying deadwood included Norway spruce, Scots pine, birch, common aspen, and others such as black alder, European ash, and rowan. Tree species were recorded as "unknown" if they could not be identified.

## Data analysis

### *Species composition and patterns in forest stand structure*

Composition coefficient of tree species were given by basal area; all coefficients are presented in Appendix 1. Species mingling (Eq. 1; Gadow, 1993) and deadwood mingling (Eq. 2; Laarmann et al., 2009), the nearest neighbourhood relationship based structural indices, were calculated to describe the segregation of different tree species and the proportion of clumped dead trees within a plot. Uniform angle (Eq. 3; Gadow & Hui, 2002) index was calculated in order to find out the proportion of irregularly positioning trees within a plot.

$$M_i = \frac{1}{k}\sum_{j=1}^{k} v_j, \quad M_i \in [0,1] \tag{1}$$

where:

$M_i$ species mingling index for reference tree *i*
tree i reference tree
tree j neighbouring tree of the reference tree *i*

$$v_j = \begin{cases} 1, \text{when species}j \neq \text{species}i \\ 0, \text{otherwise} \end{cases} \quad DM_i = \frac{1}{k}\sum_{j=1}^{k} v_j, \quad DM_i \in [0,1] \tag{2}$$

where:

$DM_i$ deadwood mingling index for reference tree *i*
treei dead reference tree
tree j neighbouring tree of the reference tree *i*

$$v_j = \begin{cases} 1, \text{when neighbour } j \text{ is a dead tree} \\ 0, \text{otherwise} \end{cases} \quad W_i = \frac{1}{k}\sum_{j=1}^{k} v_j, \quad W_i \in [0,1] \tag{3}$$

where:

$W_i$ uniform angle index for reference tree *i*;
tree i alive reference tree;
tree j neighbouring tree of the reference tree *i*;
$a_j$ angle between neighbouring trees, ≤ 180°;
$\alpha_o$ standard angle (360°/$k$ + 1), 72° when $k$ = 4 (Hui & Gadow, 2002);

**Table 1** The decay stages of lying deadwood in ENFRP assessment methodology

| Decay stage | Description |
|---|---|
| 1 | Recently, dead tree — wood is still hard and covered with bark |
| 2 | Some time ago, dead tree — the top layer of wood is still hard; bark is loose or absent |
| 3 | Weakly to medium decayed tree — slightly softened wood, knife blade penetrates up to the depth of 1 cm; bark is loose or absent |
| 4 | Very decayed tree — wood is soft; knife blade penetrates up to the depth of 5 cm |
| 5 | Almost decomposed tree — easily decomposed with bare hands |

$$v_j = \begin{cases} 1, when\ a_j < \alpha_\circ \\ 0, otherwise \end{cases}$$

Indices were calculated at the single-tree level for each tree present on the sample plot. In case with four neighbouring trees, a certain reference tree has five received values — 0, 0.25, 0.5, 0.75, and 1 (Põldveer et al., 2020). Dead trees were considered as clumped in case with index values of 0.75 and 1. Tree positioning patterns were considered as irregular in case with index values higher than 0.75, regular with value 0.5 and regular with values lower than 0.25.

Tree size heterogeneity within a sample plot was quantitatively assessed using structural complexity index (SCI; Zenner, 1998). SCI was calculated for each sample plot using ENFRP tree-level data. All standing trees present on sample plots were used for the index calculation. Tree polar coordinates were transformed into Cartesian coordinates ($x$, $y$), and dbh was used for tree size information (z).

The SCI (Eq. 4) is calculated as a ratio between the area of faceted surface SCI* (Eq. 5; three-dimensional triangles generated by tree $x$ and $y$ coordinates and $z$ coordinate according to tree dbh and its projection $A_T$):

$$\mathrm{SCI} = \frac{\mathrm{SCI}^*}{A_T}, \tag{4}$$

where $A_T$ is the sum of areas of all non-overlapping two-dimensional triangles calculated by tree $x$ and $y$ coordinates using Delaunay triangulation routine.

$$\mathrm{SCI}^* = \sum\nolimits_{i=1}^{N} \frac{1}{2}|a \times b|, \tag{5}$$

where $N$ is the number of triangles in the plot, $|a \times b|$ is the absolute value of the vector product of vector $AB$: coordinates $a = (x_b - x_a, y_b - y_a, z_b - z_a)$ and the vector $AC$: coordinates $b = (x_c - x_a, y_c - y_a, z_c - z_a)$.

Possible edge effects were corrected by omitting triangles whose nearest neighbours may locate outside the plot boundary. The triangle omitting was done by finding the midpoint between the two trees closest to the plot centre of each triangle, when the distance from the midpoint to the third or farthest tree was greater than the distance from the midpoint to the edge of the plot, then the triangle was omitted (Zenner, 2000).

*Size differences*

The age of each tree is not determined during field work because it is highly time-consuming. As tree diameter and age are strongly related (Kangur et al., 2007), the frequency distribution of tree diameters was presented to characterize the presence and frequency of different tree sizes characterising the age difference of trees. Information about skewness and kurtosis were additionally provided.

*Dead trees, lying deadwood, and large trees*

Dead trees, lying deadwood, and large trees are considered perhaps the most important structural elements in terms of providing and maintaining structural and biological diversity of forests (Põldveer, 2022). The share and volume of standing dead trees (e.g. snags) were calculated for each sample plot to provide the mean variables according to each Natura representative class. The volume of lying deadwood per hectare by tree species and decay stages were also provided, calculated as average volumes per hectare (summed volumes per hectare divided by the number of plots) by tree species and decay stages. The information about the number of large trees and large dead trees (both dbh ≥ 40 cm) per hectare were also provided.

*Gaps*

Gaps were defined as an opening in the forest canopy with minimum horizontal area 1 × 1 m. Gaps in protected forests are result from tree mortality by natural disturbances such as windthrow, insects, and fungi. A tree crown shape model (Lang & Kurvits, 2007) was used to reconstruct crowns of trees for gap size estimation. In QGis (https://www.qgis.org/en/site/), 1 × 1 m grid for the sample plot was constructed and the canopy gaps (1 m pixel) were mapped for each plot. Adjacent gaps were merged and counted as a single canopy gap. We summed the number of canopy gaps per plot and converted this to a per hectare basis for the purpose of comparable data. We calculated the area of gaps per plot ($m^2$) and determined the proportion of canopy gaps relative (%) to the size of the sample plot.

*Characteristic species*

Mosses and vascular plants — ground vegetation was described in May–August 2015 on all 100 plots in a subplot of 400 $m^2$ using the pin-point method developed by Kent and Coker (1992). Bryophyte taxonomy follows Ingerpuu et al. (1998), and vascular plant taxonomy follows Leht (2010).

Lichens and fungi were monitored on selected host material (Jõgiste et al., 2008). Samplings were done on canopy trees, co-dominant trees, dead trees or snags, fallen logs, stumps, and root-mounds in every second plot, together in 50 plots. Lichens were monitored in May–August 2015 and fungi July–November 2015.

Beetles (*Coleoptera*) were monitored with flight-intercept traps near plots. In total, there were 10 flight-intercept traps, one for every 10 sample plots locating close to each other (see Fig. 1). Traps were put on dead trees or stumps, and beetles were collected eight times (every 2 weeks) in summer 2015 and later determined in lab. Taxonomy follows Silfverberg (2010) methodology.

For a more detailed description of the species inventory methodology and results, see Appendix 2.

For conservation insights, we distinguished species of conservation concern (SPEC) according to Habitats Directive Appendix II and IV species lists, EU Habitats indicator species list (Paal, 2007; Palo, 2018), the IUCN categories (NT — near threatened, VU — vulnerable, EN — endangered, CR — critically endangered), protection category (I–III) (Estonian Government, 2004; Estonian Minister of Environment, 2004) in Estonia, and woodland key habitat (WKH) indicator species (Andersson et al., 2016).

General information about data analysis

Kruskal and Wallis (1952) nonparametric test with Dunn's (1961) multiple comparison test as a post hoc were used to assess the statistical differences of different between Natura representative classes. Data analysis was carried out in R (R Core Team, 2023) environment. The significance level was set to 0.05.

## Results

Sample plots represent Scots pine, Norway spruce, common aspen, and birch dominated stands (Table 2). A total of 40, 40, and 20 plots belong respectively to Natura representative classes A, B, and C (Table 2; see composition information from Appendix 1). The mean stand age varies from 99 years in class C to 123 years in class B. Quadratic mean diameter is between 35 and 38 cm, mean height 29–32 m, and basal area 28–34 $m^2$ per hectare in the Natura representative classes. Calculations are done based on the dominant tree layer data.

Stand characteristics (Table 2) that have statistically significant differences between Natura representative classes according to Kruskal–Wallis test are stand age ($p < 0.05$), height ($p < 0.001$), and basal area ($p = 0.01$). According to Dunn test, stand age differs between classes A–C ($p = 0.05$) and B–C ($p < 0.01$); stand height between classes A–B ($p < 0.01$), A–C ($p < 0.001$), and B–C ($p = 0.01$); and basal area between classes A–B ($p < 0.01$) and A–C ($p < 0.01$).

Different stand characteristics of the sample plots according to Natura representative classes are presented in Table 3. Stands where sample plots locate

**Table 2** General stand characteristics of the sample plots according to Natura representative classes (A, B, C): number of sample plots under observation, dominant tree species in order of frequency, and the mean age, quadratic diameter, height, and basal area of the stands sample plots locate. Tree species: SP — Scots pine (*Pinus sylvestris*), NS — Norway spruce (*Picea abies*), CA — common aspen (*Populus tremula*), BI — birch (*Betula* spp.). All means are presented with standard deviations

| Natura representative class | No of sample plots | Dominant tree species | Stand age (years) | Stand diameter (cm) | Stand height (m) | Basal area ($m^2$ $ha^{-1}$) |
|---|---|---|---|---|---|---|
| A | 40 | SP, BI, CA, NS | 113 ± 25 | 38.2 ± 6.1 | 32.1 ± 2.4 | 33.9 ± 8.7 |
| B | 40 | SP, NS | 123 ± 34 | 37.7 ± 4.3 | 30.6 ± 2.6 | 29.5 ± 6.6 |
| C | 20 | SP, NS, CA | 99 ± 21 | 35.6 ± 4.5 | 29.2 ± 2.0 | 28.0 ± 7.7 |

are relatively species rich and productive in fertile sites. The mean number of trees exceed thousand trees per hectare, being highest in class A. Mean volume of living trees exceeds 400 $m^3$ per hectare being, again, highest in class A. The volume of dead trees is also highest in class A, following by classes B and C and the proportion of dead trees follows similar trend.

Stand characteristics (Table 3) that have statistically significant differences between Natura representative classes according to Kruskal–Wallis test are volume of living trees ($p<0.001$), volume of dead trees ($p<0.01$), and share of dead trees ($p<0.001$). According to Dunn test, volume of living trees differs between classes A–B ($p<0.001$) and A-C ($p<0.001$), volume of dead trees between classes A–B ($p<0.01$) and A–C ($p=0.001$), and share of dead trees between classes A–B ($p<0.01$) and A–C ($p<0.001$).

Tree species composition (Appendix 1) showed that trees in dominant layer included Norway spruce, Scots pine, birch, common aspen, black alder, European ash, and Norway maple. Dominant trees co-occurred together with many other species. Understorey was formed mainly by Norway spruce.

To understand how different tree species mix in space, we made frequency distributions of species mingling index according to Natura representative classes (Fig. 2). Spruces, mainly understorey species, locate close to each other and experience low mingling. The trend in all three Natura representative classes is similar—the higher the species mingling index is, the less is spruce, and proportionally the more is pine, aspen, and birch represented.

Another trend can be also spotted from Fig. 2.—the higher is the Natura representative class, the lower is the species mingling index value 0. The result indicates that the higher is the Natura representative class, the less often are groups of homogeneous (in terms of species) neighbouring trees present on sampled plots.

Structural complexity index SCI was used in order to quantify the diameter variability within sample plots; higher index indicates more heterogeneous stand structure. SCI according to Natura representative classes is presented in Fig. 3. Mean SCI was highest in classes A and B (both 7.6) and lowest (6.8) in class C. Highest SCI variability was present in class C ($N=20$), followed by class A ($N=40$) and C ($N=40$).

SCI differs significantly between Natura representative classes according to Kruskal–Wallis test ($p<0.05$). The Natura classes differing statistically were A–C ($p=0.005$) and B–C ($p<0.005$) according to Dunn test.

In order to assess the spatial positioning patterns of trees, the uniform angle index was used. The proportion of irregularly, randomly, and regularly positioning trees are presented in Table 4.

Around 25% of the trees follow irregular positioning patterns in all three Natura representative classes. Most of the trees are randomly positioned. Trees are slightly more often positioned regularly, the higher is the Natura representative class, and the trend is vice versa with random positioning; however, the differences are not statistically significant ($p=0.22$ and $p=0.12$, respectively).

The diameter at breast height (dbh) distribution of living trees according to Natura representative classes is presented in Fig. 4. Aspens and pines are mostly large(r) trees and spruces mostly understorey trees despite of the representative class. Birches are about the same magnitude both understorey and co-dominant trees in class C (diameter distribution has a bimodal shape) but mainly co-dominant trees in class A and understorey trees in class B. Skewness and kurtosis information are additionally provided in Table 5 to characterize the shape of the distribution by tree species.

**Table 3** The volume and the number of trees, the share of dead trees, and the number of different tree species present on sample plots according to Natura representative classes (A, B, C). Dead trees refer to standing deadwood (e.g. snags). Means are presented with standard deviations

| Natura representative class | Volume of living trees ($m^3$ $ha^{-1}$) | Volume of dead trees ($m^3$ $ha^{-1}$) | No of all trees (pcs $ha^{-1}$) | Share of dead trees (%) | No of different tree species |
|---|---|---|---|---|---|
| A | 521 ± 101 | 30 ± 18 | 1128 ± 290 | 16 ± 7 | 4 ± 2 |
| B | 446 ± 92 | 21 ± 17 | 1078 ± 293 | 11 ± 5 | 4 ± 2 |
| C | 400 ± 97 | 16 ± 13 | 1096 ± 397 | 9 ± 5 | 5 ± 2 |

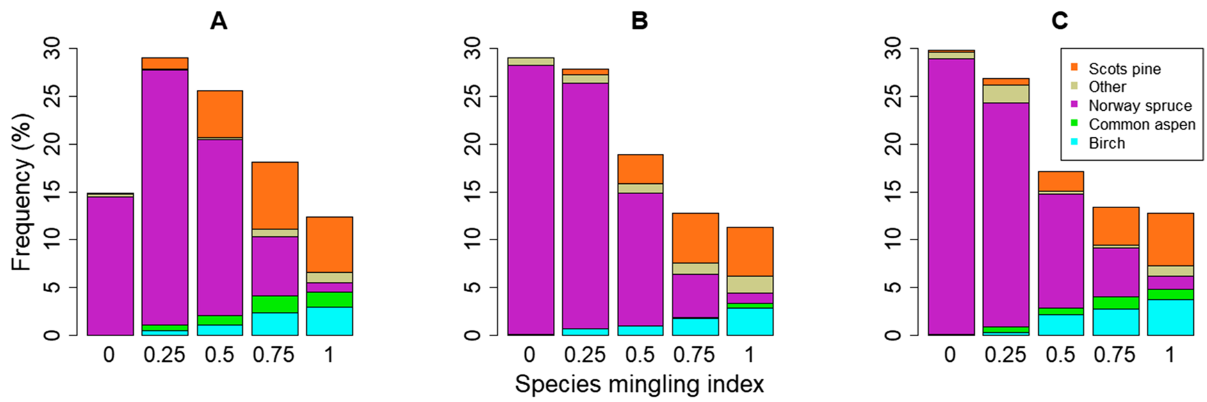


**Fig. 2** Species mingling frequency distributions according to Natura representative classes (**A**, **B**, **C**)

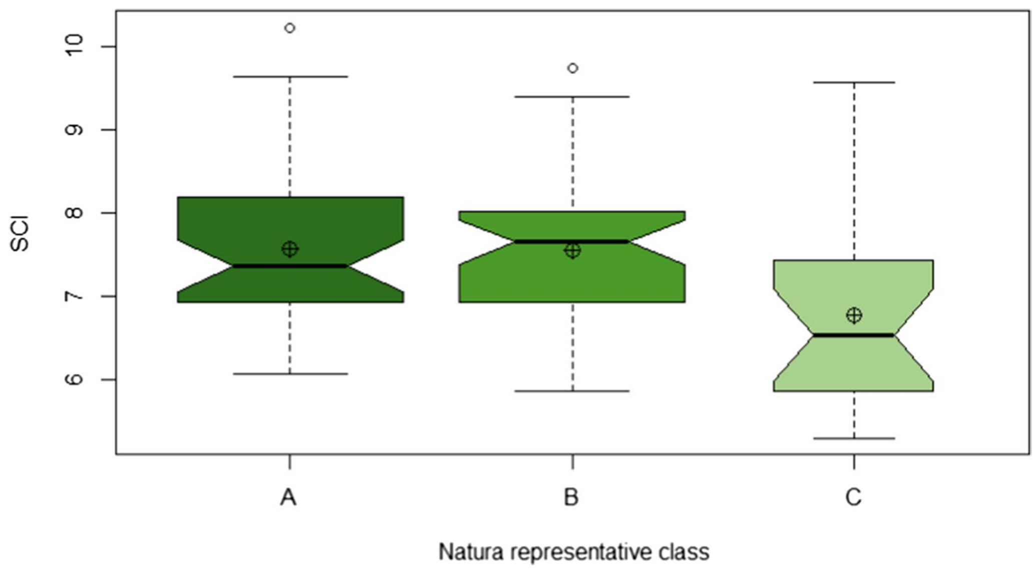


**Fig. 3** The SCI according to Natura representative classes (**A**, **B**, **C**). The solid bold black lines in the middle of each plot represent medians, crossed points means, coloured box the interquartile range (the range between first and third quartiles), empty points outliers, and black lines the minimum and maximum values of the dataset

**Table 4** The mean proportion of irregularly, randomly, and regularly positioned trees according to Natura representative classes (A, B, C). Means are presented with standard deviations

| Natura representative class | Irregularly positioned trees | Randomly positioned trees | Regularly positioned trees |
|---|---|---|---|
| A | 25.7 ± 4.8 | 53.8 ± 5.6 | 20.5 ± 4.9 |
| B | 24.3 ± 4.6 | 55.9 ± 4.2 | 19.8 ± 4.1 |
| C | 25.4 ± 3.0 | 56.3 ± 5.5 | 18.3 ± 4.8 |

The information related to large trees is presented in Table 6. Alive trees larger than (or equal) to 40 cm in dbh are present in 99% sample plots. Large trees are most frequently present in Natura representative class A and least frequently in class C. Large living trees are mostly Scots pine trees, less Norway spruce, common aspen, birch, or black alder trees. According to Kruskal–Wallis test, the amount of large trees differ between Natura

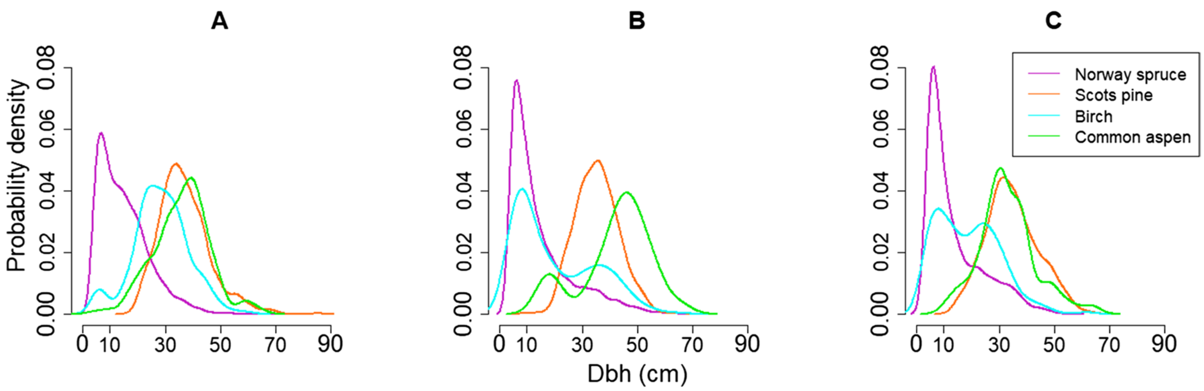


**Fig. 4** Diameter at breast height (dbh) distribution of the most common tree species by Natura representative classes (**A**, **B**, **C**)

**Table 5** Skewness and kurtosis of the diameter at breast height (dbh) distributions per tree species in Natura representative classes (A, B, C)

| | Natura representative class | | | | | |
|---|---|---|---|---|---|---|
| | A | | B | | C | |
| Tree species | Skewness | Kurtosis | Skewness | Kurtosis | Skewness | Kurtosis |
| Norway spruce | 1.08 | 1.29 | 1.52 | 1.89 | 1.29 | 0.87 |
| Scots pine | 0.89 | 1.53 | 0.23 | 0.14 | 0.30 | −0.25 |
| Birch | −0.06 | 0.32 | 0.72 | −0.69 | 0.60 | 0.05 |
| Common aspen | −0.10 | 0.45 | −0.67 | −0.3 | 0.53 | 0.70 |

representative classes ($p<0.01$). Dunn test showed that the differences occurred between groups A–C ($p=0.001$) and B–C ($p<0.01$).

Standing dead trees larger than or equal to 40 cm in dbh are present in 28% sample plots. Large standing dead trees are mostly Norway spruce trees, less Scots pine, common aspen, or birch trees. Large dead trees are most often found from class B compared to the other two classes. According to Kruskal–Wallis test, the amount of large dead trees do not differ between Natura representative classes ($p=0.22$).

Next, the clumping of dead trees is distinguished based on the deadwood mingling index (Table 7). The proportion of clumped dead trees is highest in class A where around 7% of the dead trees are clumped, followed by class B and C where the proportion of clumped dead trees was similar.

According to Kruskal–Wallis test, the proportion of clumped dead trees differ between Natura representative classes. Dunn test shows that the difference occurs between classes A–B and A–C ($p<0.001$ in case with both). Dead trees are smaller than trees on

**Table 6** The number of large trees (both, dead, and alive with dbh ≥ 40 cm) present on sample plots according to Natura representative classes (A, B, C). Dead trees refer to standing deadwood (e.g. snags). Means are presented with standard deviations

| Natura representative class | No of large trees* (pcs $ha^{-1}$) | No of large dead trees** (pcs $ha^{-1}$) |
|---|---|---|
| A | 89 ± 40 | 13 ± 8 |
| B | 82 ± 37 | 18 ± 17 |
| C | 56 ± 42 | 10 ± 3 |

*Present on 99 sample plots out of 100

** Present on 28 sample plots out of 100

average. Mean dbh of dead trees in class A is 14.4 cm (sd ± 8.3), in class B 14.8 cm (sd ± 11.4), and C 14.8 cm (± 10.5).

Lying deadwood is present in all 100 sample plots and is mostly from first and second decay stages—recently or some time ago dead trees. Lying deadwood is mostly Norway spruce, less often Scots pine, birch, common aspen, or from other species.

**Table 7** The mean proportion of dead trees positioning in a clumped pattern by Natura representative classes (A, B, C). Means are presented with standard deviations

| Natura representative class | Clumped dead trees (%) |
|---|---|
| A | 6.7 ± 13.2 |
| B | 0.6 ± 2.7 |
| C | 0.5 ± 2.1 |

The volume of lying deadwood is around 15 $m^3$ per hectare on average on first and second decay stages, and less than 5 $m^3$ per hectare on third to fifth decay stages. The volume of lying deadwood according to Natura representative classes is presented on Fig. 5.

Conifers are present in all decay stages and Natura representative classes; deciduous trees are more present in classes A and B and from first and second decay stages, whereas aspen occurs mainly in class A. The volume of lying deadwood is highest in class C (44.0 ± 43.4 $m^3$ $ha^{-1}$), followed by classes B (41.2 ± 27.4 $m^3$ $ha-^{-1}$) and A (41.0 ± 24.1 $m^3$ $ha^{-1}$) but these differences were not statistically significant ($p = 0.86$).

The proportion of canopy gaps by Natura representative classes, relative to stand area, is shown in Fig. 6. The analysis indicates a significant effect of Natura representative classes on the share of canopy gaps as a proportion of stand area. Kruskal–Wallis test shows that the proportion of gaps differs significantly between the different Natura classes ($p = 0.001$). A post hoc test reveals that the proportion of canopy gaps is significantly higher in class B (median 21%) compared to class A (median 15%) ($p < 0.001$) and significantly higher in class C (median 19%) compared to class A ($p < 0.01$). However, there is no significant difference in the proportion of canopy gaps between classes B and C ($p > 0.05$).

The analysis further shows that there is no statistically significant difference in the total number of canopy gaps between the Natura representative classes, as indicated by the Kruskal–Wallis test ($p < 0.05$). A two-factor analysis was conducted to examine the effects of Natura representative classes and gap size categories on the number of canopy gaps per stand (Fig. 7). The Dunn's test post hoc analysis shows several significant differences between the Natura classes. The average number of canopy gaps per stand is significantly lower in class B compared to class A ($p < 0.001$) and lower in class C compared to both class A ($p < 0.001$) and class B ($p = 0.01$). A significant interaction was found between Natura class and gap size categories. Specifically, the average number of canopy gaps per stand in class C and in class B for gaps > 50 $m^2$ are significantly lower than in class A for the same gap size category ($p < 0.001$). There are significant differences in the number of gaps sized 10–50 $m^2$ between Natura classes A and B and A and C ($p < 0.01$). There are significant differences in the number of small gaps (1–10 $m^2$) between A and B, also A and C Natura representative classes ($p < 0.05$). But there is no significant differences between B and C in both gap size classes—1–10 $m^2$ and 10–50 $m^2$. These results indicate that both Natura representative classes and gap size categories influence the number of canopy gaps per stand, with class C consistently showing fewer gaps than classes

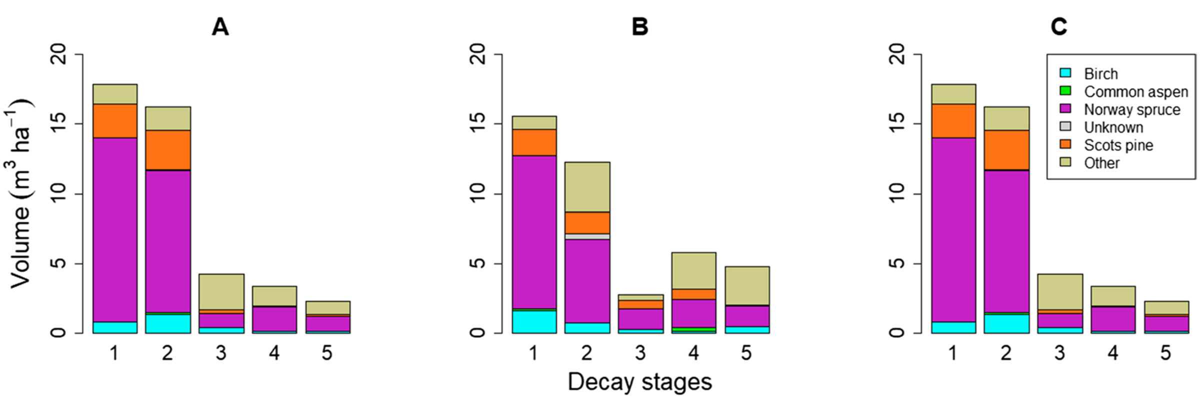


**Fig. 5** The volume of lying deadwood according to tree species and decay stages by Natura representative classes (**A**, **B**, **C**)

A and B, particularly for larger gap sizes (> 50 $m^2$). Figures 6 and 7 suggest a notable variation in the distribution of gap sizes across the different Natura representative classes, particularly in the number of small and medium-sized gaps.

The total of 296 vascular plant and bryophyte species were identified on plots—167 herb, 24 tree and bush, and 105 moss species. On every second plot, there were a total of 157 lichen and 48 polypore fungi species present. Most of the lichen species are found on birch (average 16 species), followed by pine, spruce (14 species), and spruce logs and black alder (13 species). On average, there are six polypore fungi species on plot, and *Trichaptum abietinum*, *Fomitopsis pinicola*, and *Phellinus tremula* are the most common ones. A total of 366 beetle species were found on flight-intercept traps and 138 species for site on average. Sixty-three forest-dwelling SPEC species were distinguished (Table 8) including seven vascular plants, 12 mosses, 17 lichens, 11 fungi, and 16 beetles. No species according to Habitats Directive species lists (Appendixes II and IV) are present but all other criteria are.

Overall, there are SPEC species on all plots: mosses on 82% of the plots (A 90%, B 78%, C 75% based on relative frequency), vascular plants on 44% of the plots (A 48%, B 45%, C 35%), lichens on 74% of the plots (A 70%, B 80%, C 70%), fungi on 54% of the plots (A 55%, B 60%, C 40%), and beetles on 100% of the plots (all 100%).

## Discussion

The Natura 2000 network plays an important role in achieving the conservation targets set by the European Green Deal (2023) and the EU Biodiversity Strategy for, 2030 (2020). Protecting representative habitat types, such as the Western Taiga (*9010), and ensuring their development across various stages are fundamental for biodiversity conservation in Estonia (Lõhmus et al., 2004). However, despite these efforts, only 15% of Natura 2000 habitats are classified as being in favourable condition (European Commission, 2020). Achieving the desired conservation status for (hemi)boreal forests,

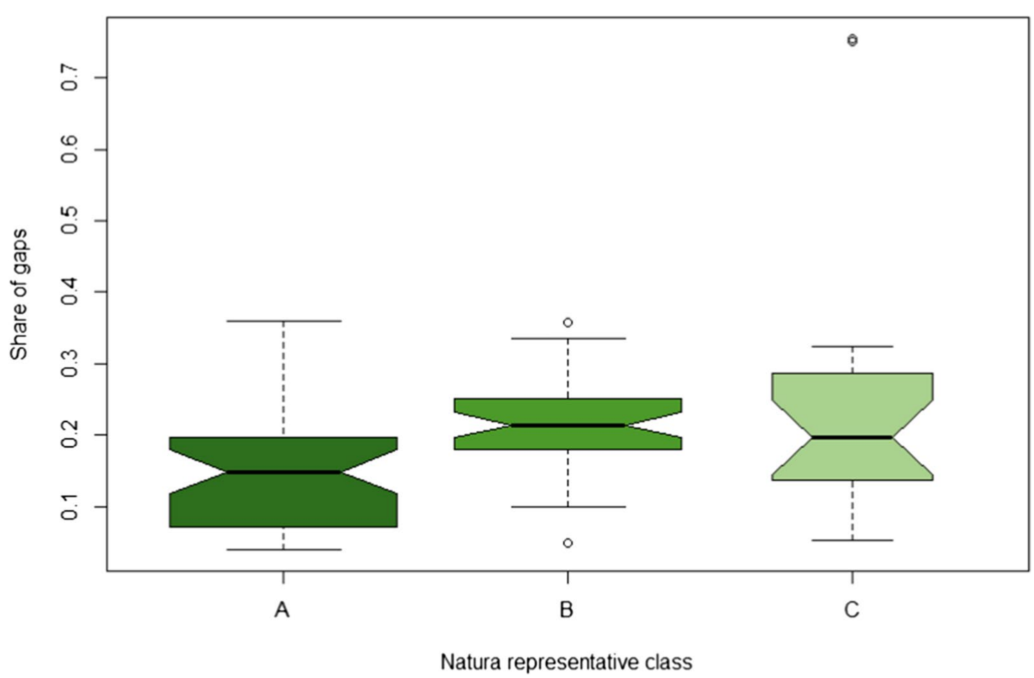


**Fig. 6** The share of canopy gaps by Natura representative classes (**A**, **B**, **C**) as a proportion of stand area. The solid bold black lines in the middle of each plot represent medians, coloured box the interquartile range (the range between first and third quartiles), empty points outliers, and black lines the minimum and maximum values of the dataset

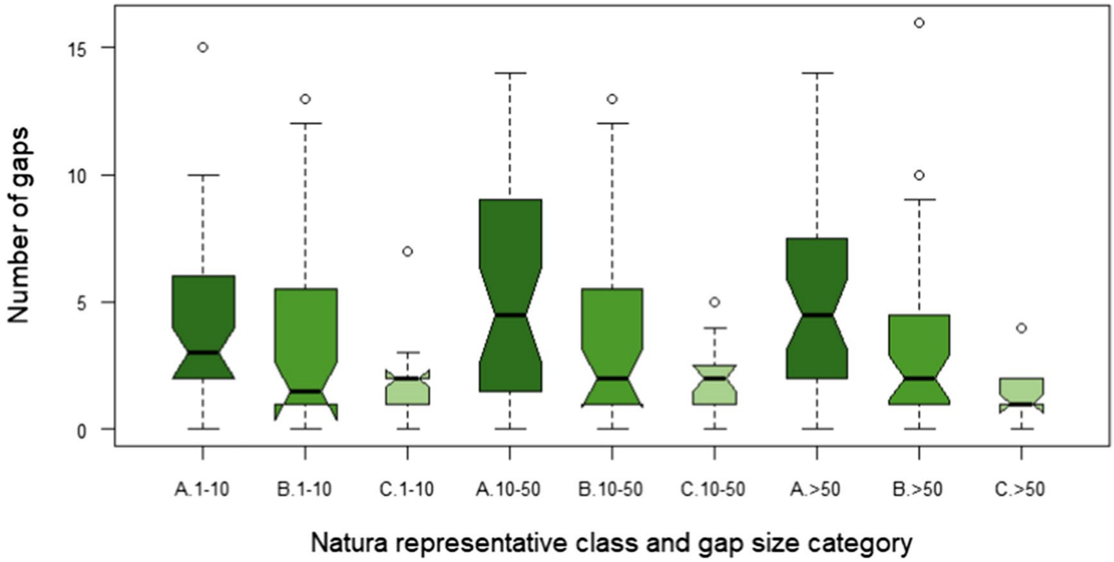


**Fig. 7** Distribution of average gap sizes (1–10 $m^2$, 10–50 $m^2$, > 50 $m^2$) per stand by Natura representative classes (**A**, **B**, **C**). The solid bold black lines in the middle of each plot represent medians, coloured box the interquartile range (the range between first and third quartiles), empty points outliers, and black lines the minimum and maximum values of the dataset. The notches extend beyond the hinges because the sample size is relatively small and variability high, resulting in a wider confidence interval around the median

including the Western Taiga, requires an increasing emphasis on preserving and enhancing old-growth forest characteristics (Berglund & Kuuluvainen, 2021).

In current study, several methods were proposed and applied to assess the structural heterogeneity and ecological quality of the Western Taiga habitats in Estonia. The results provide valuable insights into habitat conditions, with implications for improving the conservation and management of these unique ecosystems. Based on the results of the research article, several conclusions can be drawn.

### Structural heterogeneity and ecological quality

One of the primary objectives of the study was to assess the structural diversity of Western Taiga habitats, particularly in relation to their conservation status (Natura representative class). The findings suggest that structural complexity plays a significant role in maintaining ecological integrity in Western Taiga habitats, which is further supported by previous research by Franklin and van Pelt (2004). Their research highlights the importance of maintaining old-growth characteristics such as deadwood, large trees, and variable age structures for biodiversity. In Estonia, these structural features are generally represented in protected forests (Põldveer et al., 2020, 2021).

Key structural elements, such as the presence of large living and dead trees, played an important role in the habitat. Large trees, including those from previous generations, were observed in all Natura representative classes, contributing to the overall structural complexity. Large living trees were present in 99% of the sample plots, with Scots pine being the most dominant species. Large dead trees, predominantly Norway spruce, were also present in all representative classes, occurring in 28% of the sample plots. These large dead trees are essential for coarse woody debris (also known as CWD) formation, which is vital for nutrient cycling and provides important habitats for a variety of organisms (Tikkanen et al., 2006).

Natura representative class A habitats demonstrated the highest structural complexity in this study, as indicated by the greater volume of deadwood,

**Table 8** Species with conservation concern (SPEC) of mosses (M), vascular plants (V), lichens (L), fungi (F), and beetles (B) in different Natura representative classes (A, B, C) based on relative frequency and abundance of given species. Criteria: I — EU habitat indicator (Paal, 2007; Palo, 2018); WKH — woodland key habitat indicator (Andersson et al., 2016); the IUCN categories (NT — near threatened, VU — vulnerable, EN — endangered, CR — critically endangered) and protection category of Estonia (C1, C2, C3)

| Species | Group | Conservation status | % of plots in given class where given species is present | | | |
|---|---|---|---|---|---|---|
| | | | A | B | C | In all |
| *Anastrophyllum hellerianum* | M | I, WKH, C3 | 10 | 8 | 0 | 7 |
| *Hylocomium umbratum* | M | I, WKH, VU | 3 | 0 | 0 | 1 |
| *Jamesoniella autumnalis* | M | I, WKH | 3 | 15 | 15 | 10 |
| *Lepidozia reptans* | M | I, WKH | 28 | 35 | 25 | 30 |
| *Neckera pennata* | M | I, WKH, C3 | 10 | 13 | 5 | 10 |
| *Nowellia curvifolia* | M | I, WKH | 60 | 35 | 40 | 46 |
| *Plagiothecium latebricola* | M | I | 3 | 0 | 0 | 1 |
| *Riccardia latifrons* | M | I, WKH | 0 | 8 | 10 | 5 |
| *Riccardia palmata* | M | I, WKH | 3 | 3 | 0 | 2 |
| *Sphagnum wulfianum* | M | I, WKH, C3 | 0 | 0 | 10 | 2 |
| *Tetraphis pellucida* | M | WKH | 45 | 48 | 50 | 47 |
| *Ulota crispa* | M | I, WKH | 25 | 20 | 0 | 18 |
| *Dactylorhiza fuchsii* | V | C3 | 0 | 18 | 0 | 7 |
| *Dactylorhiza maculata* | V | C3 | 0 | 3 | 0 | 1 |
| *Goodyera repens* | V | C3 | 48 | 28 | 25 | 35 |
| *Listera ovata* | V | C3 | 0 | 3 | 0 | 1 |
| *Platanthera bifolia* | V | C3 | 0 | 0 | 10 | 2 |
| *Platanthera* sp. | V | C3 | 0 | 0 | 5 | 1 |
| *Pleurospermum austriacum* | V | C2 | 0 | 3 | 0 | 1 |
| *Acrocordia cavata* | L | I, WKH | 5 | 50 | 50 | 32 |
| *Alyxoria varia* | L | WKH, VU | 20 | 40 | 10 | 26 |
| *Arthonia leucopellaea* | L | I, WKH | 10 | 40 | 10 | 22 |
| *Arthonia vinosa* | L | I, WKH | 0 | 30 | 0 | 12 |
| *Bacidia rubella* | L | I, WKH | 5 | 15 | 10 | 10 |
| *Carbonicola anthracophila* | L | WKH, C2, VU | 15 | 5 | 10 | 10 |
| *Chaenotheca brachypoda* | L | I, WKH | 5 | 15 | 0 | 8 |
| *Chaenotheca gracillima* | L | I, WKH, NT | 0 | 5 | 0 | 2 |
| *Hypogymnia farinacea* | L | I, WKH | 0 | 5 | 0 | 2 |
| *Lecanactis abietina* | L | C3, NT | 0 | 5 | 0 | 2 |
| *Lecidea erythrophaea* | L | WKH, C3 | 5 | 0 | 0 | 2 |
| *Leptogium saturninum* | L | I, C3, VU | 25 | 15 | 10 | 18 |
| *Megalaria grossa* | L | C2, VU | 5 | 5 | 0 | 4 |
| *Micarea hedlundii* | L | I, WKH | 0 | 5 | 10 | 4 |
| *Mycoblastus sanguinarius* | L | I, NT | 0 | 10 | 0 | 4 |
| *Opegrapha vulgata* | L | C2, VU | 5 | 0 | 0 | 2 |
| *Scytinium teretiusculum* | L | I | 10 | 5 | 0 | 6 |
| *Asterodon ferruginosus* | F | I, WKH | 0 | 5 | 0 | 2 |
| *Fomitopsis rosea* | F | I, WKH | 10 | 20 | 15 | 18 |
| *Phellinus chrysoloma* | F | I,WKH | 10 | 0 | 0 | 4 |
| *Phellinus ferrugineofuscus* | F | I, WKH | 20 | 40 | 10 | 28 |
| *Phellinus nigrolimitatus* | F | WKH | 10 | 0 | 0 | 4 |
| *Phellinus populicola* | F | I, WKH | 5 | 5 | 5 | 6 |
| *Phellodon tomentosus* | F | I, WKH | 5 | 0 | 0 | 2 |
| *Phlebia centrifuga* | F | I, WKH | 5 | 15 | 0 | 8 |

**Table 8** (continued)

| Species | Group | Conservation status | % of plots in given class where given species is present | | | |
|---|---|---|---|---|---|---|
| | | | A | B | C | In all |
| *Pycnoporellus fulgens* | F | I, WKH | 20 | 20 | 10 | 20 |
| *Rigidoporus crocatus* | F | WKH, C3 | 0 | 5 | 0 | 2 |
| *Skeletocutis odora* | F | VU | 0 | 5 | 0 | 2 |
| *Callidium coriaceum* | B | WKH | 0 | 25 | 0 | 20 |
| *Dendrophagus crenatus* | B | WKH | 25 | 25 | 50 | 30 |
| *Isorhipis marmottani* | B | I | 0 | 25 | 0 | 10 |
| *Mycetochara axillaris* | B | WKH | 25 | 0 | 0 | 10 |
| *Mycetochara flavipes* | B | WKH | 25 | 100 | 50 | 60 |
| *Mycetochara obscura* | B | WKH | 50 | 50 | 50 | 50 |
| *Mycetophagus quadripustulatus* | B | WKH | 100 | 100 | 100 | 100 |
| *Necydalis major* | B | WKH | 0 | 25 | 0 | 10 |
| *Ostoma ferruginea* | B | WKH | 50 | 75 | 100 | 70 |
| *Pachyta lamed* | B | I | 0 | 25 | 0 | 10 |
| *Peltis grossa* | B | WKH | 0 | 25 | 0 | 10 |
| *Pityophthorus morosovi* | B | I | 25 | 0 | 0 | 10 |
| *Platycerus caprea* | B | I | 25 | 0 | 0 | 10 |
| *Pytho abieticola* | B | I | 25 | 0 | 0 | 10 |
| *Triphyllus bicolor* | B | I | 50 | 50 | 0 | 40 |
| *Xylita livida* | B | I | 0 | 25 | 0 | 10 |

larger trees, and a higher number of canopy gaps. Structural diversity supports greater ecological resilience and provides essential habitats for a wide range of species (Seidel et al., 2019). The study also showed that at least 25% of the trees exhibited irregular positioning patterns, regardless of the Natura representative class. These irregularly positioned trees, along with the deadwood and gaps, contribute to the heterogeneous forest structure. Although the proportion of irregularly positioned trees was similar across all classes, this irregularity remains an important factor in promoting structural diversity. Irregular tree spacing is often associated with more natural, unmanaged forests (Põldveer et al., 2020), where competition and natural disturbances (such as tree falls and gaps) shape the forest landscape over time.

The Structural Complexity Index (SCI), which reflects the overall stand structural diversity, differed significantly across Natura representative classes, with class A and class B showing higher values than class C. These results indicate that class C habitats are less structurally diverse and may require targeted restoration efforts to enhance their ecological function. High structural heterogeneity provides a diversity of ecological niches (McElhinny et al., 2005), thereby supporting a broader range of species and increasing overall biodiversity.

Structural indicators such as the abundance of large trees, deadwood volume, canopy gaps, and others can serve as decision-support tools for both managed and unmanaged forests. In actively managed forests, indicators can help guide logging practices that maintain ecological functions. In conservation areas and unmanaged stands, they provide a benchmark to assess whether passive protection is sufficient or if additional measures (e.g. deadwood retention, controlled disturbances) are needed to support biodiversity and ecosystem resilience. Since structural complexity varied significantly across Natura representative classes, indicators can help identify where targeted restoration efforts may be needed, particularly in class C habitats. By integrating structural indicators into broader forest management decisions, including those made in commercial forests, both the ecological quality and long-term sustainability of Western Taiga habitats can be enhanced.

## Dead wood, canopy gaps, and their ecological importance

The presence of dead trees and snags is closely linked to the formation of canopy gaps (Franklin & van Pelt, 2004), playing a vital role in shaping forest structure and promoting ecological diversity. Coarse woody debris is particularly important for a wide range of species, serving as a substrate for various organisms. Factors such as substrate availability (Ingerpuu, 2002; Lõhmus et al., 2007; Weibull, 2001), composition, and quality (Botting & DeLong, 2009; Kumar et al., 2016) are important in determining the ecological value of coarse woody debris. Environmental variables such as soil nutrients, moisture, and acidity significantly influence the decomposition process and the role of deadwood in forest ecosystems (Jüriado et al., 2016).

In the current study, most of the dead trees observed were smaller in size, with competition being the primary cause of tree mortality. The clumping of dead trees was a frequent occurrence, which serves as the basis for future gap formation (Laarmann et al., 2009). This process of natural disturbance is essential for maintaining forest dynamics, as the formation of gaps creates microhabitats that support species diversity, particularly for light-demanding species and regenerating seedlings. The study also observed the flow of lying deadwood, which had accumulated over long periods. Deadwood from different tree species was found in various stages of decay, with all five decay stages present across all Natura representative classes. The presence of deadwood in different stages of decomposition is needed for the nutrient cycling process and provides a range of ecological niches, supporting species that rely on deadwood for habitat (Lasota et al., 2018).

The analysis of canopy gaps revealed significant differences in gap characteristics between the Natura representative classes. The results indicated that class B and class C had a higher proportion of canopy gaps compared to class A, suggesting that disturbances (natural or anthropogenic) may play a more significant role in shaping Western Taiga habitats. This also suggests that forest development stages (Franklin et al., 2002) have progressed, moving from a maturation stage towards increased vertical and horizontal diversification. The study also demonstrated that larger gaps ($> 50$ m$^2$) were significantly less frequent in class C compared to class A. This aligns with the idea that larger gaps are important for maintaining ecosystem health by contributing to increased light availability and regeneration potential. Class C had fewer large gaps, which may explain its lower overall biodiversity and ecological value. These findings indicate that larger canopy openings are essential for maintaining forest structural diversity, enhancing biodiversity, and increasing resilience to environmental change. The absence of significant differences in the number of small gaps (1–10 m$^2$) between the classes indicates that smaller disturbances are more evenly distributed across the habitats, suggesting a potential area for further research. Gaps are essential for forest regeneration and biodiversity, providing opportunities for light-demanding species and creating a dynamic mosaic of forest patches (Kuuluvainen et al., 2021).

## The presence of characteristic species

Characteristic species serve as valuable indicators for evaluating the health and quality of ecosystems (Dale & Beyeler, 2001; Carigan et al., 2002). These species act as ecological sentinels, providing insights into environmental conditions and the overall state of ecosystem health (Hermy et al., 1999; Lindenmayer et al., 2000). Their presence is particularly important in ecological studies, as they can signal changes in the environment and contribute to our understanding of biodiversity patterns (Siddig et al., 2016).

The distribution of characteristic species across different Natura representative classes demonstrated the ecological diversity within the habitat. Class A habitats were found to have the highest conservation significance, as they support a relatively higher abundance of SPEC species (Species of European

Conservation Concern), including key WKH (Woodland Key Habitat) indicator species. Class B habitats also exhibited substantial biodiversity and conservation value, although to a lesser extent than class A. In contrast, class C habitats, while still contributing to regional biodiversity, supported fewer SPEC species and showed lower relative frequencies of these characteristic species.

These findings suggest that conservation strategies must be tailored to address the specific ecological characteristics and needs of each Natura class. Targeted conservation efforts in class A and B habitats will be essential to preserve their high biodiversity value, while restoration and management interventions in class C should focus on enhancing species diversity and supporting the presence of characteristic species to improve the overall ecological integrity of these habitats.

### Implications for forest management and policy

The results of this study have significant implications for forest management and conservation policy, both in Estonia and across Europe. Class A habitats are in good conservation status, and these areas are already under strict protection. However, the lower ecological quality observed in class C habitats suggests that these areas may benefit from targeted management interventions, such as promoting natural disturbance regimes or enhancing the retention of structural indicators, e.g. deadwood and large trees. To ensure the long-term ecological quality of these habitats, a balanced approach is needed—one that integrates economic objectives with ecosystem integrity, particularly in the context of the growing demand for biomass. The effectiveness of such an approach largely depends on the engagement of private forest owners, who play the key role in forest management across Europe.

There are about 16 million private forest owners in Europe (EU Forest Strategy for, 2030, 2021) and over 100,000 in Estonia (Estonian Environmental Agency, 2022). Their attitudes towards nature protection, along with their understanding of effective habitat conservation practices, play a key role in ensuring the ecological quality of forests. A study carried out in Estonia by Suškevičs and Külvik (2007) showed challenges, including negative attitudes towards the Natura 2000 network among private landowners, largely due to issues related to ineffective compensation measures. Without adequate incentives, private landowners may prioritize economic gains over conservation, as seen in Germany (Tiebel et al., 2021). This example underscores the importance of adequate compensation mechanisms to motivate private landowners to engage in nature conservation, as well as the need to enhance their awareness of how to support and maintain forest biodiversity.

### Conservation strategies and recommendations

Passive protection of forest habitats is not always sufficient, and it may not be necessary to completely prohibit human activity within Natura 2000 forest habitats. In certain cases, forest owners could be permitted to conduct selective cuttings within protected areas, particularly when the habitat has not yet reached Class A quality. These cuttings, carefully planned and carried out in consultation with specialists, could serve as a restoration tool to accelerate the development of structurally diverse forests. By enhancing key structural elements such as large trees, deadwood, and canopy gaps, these interventions would contribute to improving habitat complexity and ecological resilience. Appropriate official guidelines should be developed to facilitate this approach.

To improve the conservation status of Western Taiga habitats, particularly in class B and class C, forest managers should focus on enhancing structural diversity. This can be achieved through measures such as increasing the retention of large trees, promoting natural disturbances, and ensuring the presence of coarse woody debris. These structural elements play a key role in restoring habitats to a more favourable conservation status. Additionally, creating and maintaining canopy gaps of varying sizes will provide opportunities for regeneration and species colonization, further promoting biodiversity.

Conservation strategies must also address more the socio-economic realities of private forest ownership. Given the scale of private land ownership in Europe and Estonia, it is essential that incentive programs are developed to support sustainable forest management practices. These programs, coupled with effective compensation mechanisms, would encourage private forest owners to adopt practices that enhance structural diversity of their forests and contribute to the broader conservation goals of Natura 2000.

Policy recommendations should focus on creating a supportive framework for private landowners, ensuring that they are not penalized for conservation efforts but instead incentivized to contribute to biodiversity conservation. The lessons from Germany (Tiebel et al., 2021) illustrate the risks of restrictive management approaches that alienate landowners. By engaging private forest owners and aligning their economic interests with conservation objectives, it is possible to foster a more collaborative and effective approach to habitat protection.

## Conclusions

In conclusion, the Western Taiga habitat represents a highly variable and ecologically valuable ecosystem within Estonia's Natura 2000 network. This study demonstrates that structural diversity plays a key role in determining conservation status. While class A habitats are in good condition, classes B and C may require targeted management efforts to improve their structural complexity and ecological value. The findings of the study provide important guidelines for forest management and highlight the need for ecosystem-based approaches that balance economic and ecological objectives. Achieving different goals will be essential for meeting the EU's biodiversity targets and ensuring the long-term sustainability of Western Taiga forest habitats.

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**Author contribution** E.P. wrote the main manuscript text. D.L. edited and made additions to the manuscript text. E.P. prepared tables and Figs. 1–5, D.L prepared Figs. 6–7. E.P., D.L and T.A. carried out data analysis. T.P. conducted fieldworks. All authors contributed to the development of the article's structure and reviewed the manuscript.

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**Data availability** No datasets were generated or analysed during the current study.

**Declarations**

**Ethical Approval** All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

**Competing interests** The authors declare no competing interests.

## Appendix 1

Species composition, Natura 2000 habitat quality assessments (from EELIS (2014) database and during fieldworks, management operations carried out on sample plots and different characteristics for each sample plot. No — sample plot number, tree species: SP — Scots pine (*Pinus sylvestris*); NS — Norway spruce (*Picea abies*); CA — common aspen (*Populus tremula*); BI — birch (*Betula* spp.); BA — black alder (*Alnus glutinosa*); EA — European ash (*Fraxinus excelsior*); NM — Norway maple (*Acer platanoides*). Management history and harvesting method: S — selective felling, SR — sanitary felling, LT — late thinning, T — thinning, CT — pre-commercial thinning, NR — facilitating natural regeneration or site preparation for natural regeneration. Large trees dbh ≥ 40 cm

| No | Composition | Natura assessment | Management history | No of large trees (ha$^{-1}$) | No of large dead trees (ha$^{-1}$) | Share of dead trees (%) | Share of clumped dead trees (%) | Volume of lying deadwood (m$^3$ ha$^{-1}$) | Share of irregularly positioning trees (%) | SCI |
|---|---|---|---|---|---|---|---|---|---|---|
| 1614 | 63SP31NS6BI | A | T1952 | 96 | 0 | 8.5 | 0.0 | 8.2 | 33.1 | 7.95 |
| 1615 | 60SP24BI16NS | A | T1952 | 96 | 24 | 11.0 | 0.0 | 51.2 | 25.4 | 7.79 |
| 1616 | 76SP14NS10BI | A | LT1951 | 112 | 0 | 25.0 | 9.1 | 30.8 | 25.3 | 7.43 |
| 1617 | 92SP7NS1BI | A | LT1951 | 119 | 0 | 19.0 | 8.3 | 85.0 | 24.5 | 6.76 |
| 1618 | 77SP23NS | A | LT1951 | 156 | 0 | 16.7 | 0.0 | 45.0 | 24.6 | 10.22 |
| 1619 | 98SP2NS | A | LT1951 | 48 | 0 | 11.0 | 0.0 | 28.4 | 24.0 | 7.30 |
| 1620 | 76SP21NS3BI | A | | 56 | 8 | 19.9 | 13.9 | 90.7 | 24.8 | 6.96 |
| 1621 | 100SP | A | NR1948 | 48 | 0 | 11.8 | 0.0 | 75.8 | 25.7 | 6.37 |
| 1622 | 85SP13NS2BI | A | NR1948 | 24 | 0 | 16.7 | 14.3 | 66.8 | 23.6 | 6.46 |
| 1623 | 97SP2NS1BI | A | | 48 | 0 | 23.2 | 6.4 | 54.3 | 25.6 | 6.89 |
| 1624 | 42SP39BI18NS | A | CT1948 | 170 | 0 | 7.5 | 0.0 | 14.6 | 25.0 | 9.64 |
| 1625 | 96SP4NS | A | | 64 | 0 | 21.9 | 0.0 | 66.5 | 16.9 | 7.24 |
| 1626 | 66SP24NS10BI | A | T1952 | 96 | 0 | 17.0 | 0.0 | 68.0 | 24.4 | 7.42 |
| 1627 | 50SP20NS16BI14CA | A | T1952 | 96 | 0 | 10.1 | 0.0 | 40.5 | 18.9 | 7.59 |
| 1628 | 73SP24NS3BI | A | T1952 | 88 | 0 | 14.4 | 0.0 | 62.4 | 23.9 | 8.34 |
| 1629 | 65SP30NS3BI2CA | A | | 56 | 0 | 22.6 | 0.0 | 55.6 | 19.5 | 7.49 |
| 1630 | 98SP2NS | A | S1963 | 43 | 0 | 11.3 | 0.0 | 61.1 | 40.3 | 8.13 |
| 1631 | 69SP23NS4BI4CA | A | | 80 | 0 | 16.8 | 4.8 | 64.4 | 23.1 | 7.85 |
| 1632 | 70BI13CA11NS6SP | A | T1952 | 85 | 0 | 12.9 | 44.4 | 53.8 | 23.0 | 6.81 |
| 1633 | 49SP21BI17CA13NS | A | T1952 | 72 | 0 | 13.6 | 0.0 | 22.4 | 30.6 | 7.28 |
| 1634 | 66SP34NS | B | SR1986, T1986 | 24 | 0 | 6.2 | 0.0 | 35.3 | 32.0 | 6.82 |
| 1635 | 72SP28NS | B | SR1986, T1986 | 96 | 0 | 5.1 | 0.0 | 60.6 | 24.8 | 8.06 |
| 1636 | 61SP39NS | B | SR1986, T1986, SR2002 | 80 | 0 | 13.5 | 0.0 | 37.7 | 23.7 | 8.42 |
| 1637 | 63SP30NS7BI | B | SR1986, T1986, SR2002 | 96 | 0 | 9.3 | 0.0 | 16.7 | 25.7 | 7.73 |
| 1638 | 72SP20NS8BI | B | SR1986, T1986, SR2002 | 112 | 0 | 7.9 | 0.0 | 44.8 | 22.1 | 8.48 |
| 1639 | 43SP40NS17BI | B | SR1986, T1986, SR2002 | 119 | 16 | 9.2 | 0.0 | 33.2 | 22.5 | 8.42 |
| 1640 | 87SP8BI5NS | B | SR1986, T1986, SR2002 | 56 | 0 | 9.6 | 0.0 | 19.5 | 16.8 | 6.88 |
| 1641 | 68SP32NS | B | SR1986, T1986, SR2002 | 112 | 0 | 9.2 | 0.0 | 39.2 | 26.1 | 8.17 |
| 1642 | 90SP6NS4BI | B | SR1986, T1986, SR2002 | 40 | 0 | 19.5 | 0.0 | 26.8 | 21.0 | 7.48 |
| 1643 | 76SP24NS | B | SR1986, T1986, SR2002 | 48 | 0 | 15.5 | 0.0 | 22.3 | 20.4 | 6.89 |
| 1644 | 93SP7NS | B | SR1986, T1986 | 72 | 0 | 19.0 | 15.8 | 20.6 | 18.5 | 7.17 |
| 1645 | 85SP15BI | B | | 32 | 0 | 24.7 | 5.6 | 37.6 | 27.3 | 6.06 |
| 1646 | 58SP32BI10NS | B | | 96 | 0 | 13.8 | 0.0 | 84.2 | 23.9 | 8.05 |
| 1647 | 76SP21NS3BI | B | SR1985, T1985 | 96 | 0 | 8.7 | 0.0 | 19.6 | 32.7 | 7.26 |

| No | Composition | Natura assessment | Management history | No of large trees (ha$^{-1}$) | No of large dead trees (ha$^{-1}$) | Share of dead trees (%) | Share of clumped dead trees (%) | Volume of lying deadwood (m$^3$ ha$^{-1}$) | Share of irregularly positioning trees (%) | SCI |
|---|---|---|---|---|---|---|---|---|---|---|
| 1648 | 93SP5BI2NS | B | SR1985, T1985 | 143 | 0 | 8.7 | 0.0 | 20.0 | 30.7 | 8.46 |
| 1649 | 64SP24BI12NS | B | | 112 | 8 | 22.2 | 2.9 | 24.0 | 12.6 | 7.68 |
| 1650 | 70SP20BI10NS | B | SR1985, T1985 | 96 | 0 | 16.8 | 0.0 | 43.2 | 23.9 | 7.96 |
| 1651 | 62SP22BI16NS | B | SR1985, T1985 | 112 | 0 | 16.8 | 0.0 | 21.5 | 21.1 | 7.92 |
| 1652 | 98SP1BI1NS | B | | 72 | 0 | 13.9 | 0.0 | 13.4 | 20.0 | 7.97 |
| 1653 | 97SP2BI1NS | B | | 8 | 0 | 14.9 | 0.0 | 19.9 | 30.0 | 7.68 |
| 1654 | 100SP | A | S1994, SR2011, SR2014 | 156 | 0 | 3.8 | 0.0 | 2.9 | 27.1 | 8.27 |
| 1655 | 84SP16NS | A | S1994, SR2011, SR2014 | 80 | 8 | 6.0 | 0.0 | 24.8 | 35.6 | 7.04 |
| 1656 | 97SP3NS | A | S1994, SR2011, SR2014 | 113 | 0 | 8.5 | 0.0 | 18.9 | 27.3 | 7.49 |
| 1657 | 94SP6NS | A | S1994, SR2011, SR2014 | 127 | 0 | 3.3 | 0.0 | 1.4 | 33.3 | 8.75 |
| 1658 | 92SP8NS | A | S1994, SR2011, SR2014 | 85 | 0 | 10.3 | 66.7 | 15.7 | 25.0 | 6.08 |
| 1659 | 84SP16NS | A | S1994, SR2011, SR2014 | 112 | 0 | 9.6 | 0.0 | 50.3 | 24.2 | 8.73 |
| 1660 | 91SP9NS | A | S1994, SR2011, SR2014 | 159 | 8 | 8.7 | 0.0 | 32.1 | 22.7 | 8.88 |
| 1661 | 82SP18NS | A | S1994, SR2011, SR2014 | 119 | 0 | 6.8 | 0.0 | 9.0 | 30.1 | 6.99 |
| 1662 | 92SP8NS | A | S1994, SR2011, SR2014 | 127 | 0 | 4.5 | 0.0 | 3.4 | 34.5 | 7.01 |
| 1663 | 85SP14NS1BI | A | | 119 | 8 | 21.4 | 20.0 | 56.3 | 25.3 | 8.85 |
| 1664 | 74BI26NS | A | CT1956 | 43 | 0 | 22.2 | 0.0 | 38.0 | 23.8 | 8.25 |
| 1665 | 65NS31SP4BI | A | CT1956 | 32 | 0 | 22.1 | 3.3 | 33.9 | 25.5 | 7.09 |
| 1666 | 49BI48CA4NS | A | CT1956 | 48 | 0 | 17.4 | 0.0 | 39.7 | 31.6 | 6.43 |
| 1667 | 85CA10BI3NS2SP | A | CT1956 | 96 | 0 | 22.5 | 0.0 | 30.9 | 24.8 | 6.94 |
| 1668 | 82CA12BI6NS | A | CT1956 | 96 | 0 | 22.4 | 2.7 | 22.4 | 19.5 | 7.43 |
| 1669 | 56BI29CA15NS | A | CT1956 | 40 | 0 | 28.8 | 15.9 | 50.0 | 26.6 | 6.91 |
| 1670 | 85BI11NS3CA1SP | A | CT1956 | 32 | 8 | 24.5 | 18.4 | 37.2 | 25.2 | 7.29 |
| 1671 | 92CA6BI2NS | A | T1956 | 151 | 0 | 19.7 | 11.4 | 29.6 | 23.0 | 9.47 |
| 1672 | 71CA16BI13NS | A | T1956 | 48 | 24 | 21.1 | 17.4 | 82.6 | 17.4 | 6.15 |
| 1673 | 68CA15NS12BI5SP | A | T1956 | 119 | 0 | 25.2 | 9.7 | 13.1 | 25.0 | 6.53 |
| 1674 | 49NS30SP20BI1BA | C | LT1957, LT1964 | 16 | 8 | 8.1 | 0.0 | 54.0 | 28.1 | 5.74 |
| 1675 | 83SP13NS4BI | C | LT1957, LT1964 | 56 | 0 | 5.5 | 0.0 | 59.1 | 20.7 | 8.33 |
| 1676 | 55NS39SP6BI | C | LT1957, LT1964 | 56 | 8 | 11.3 | 0.0 | 68.8 | 31.0 | 6.59 |
| 1677 | 44NS32SP24BI | C | LT1957, LT1964 | 80 | 8 | 12.5 | 0.0 | 84.2 | 28.6 | 6.46 |
| 1678 | 86SP14NS | C | LT1957, LT1964 | 183 | 0 | 8.2 | 0.0 | 114.2 | 26.0 | 9.56 |
| 1679 | 70SP30NS | C | LT1957, LT1964 | 119 | 8 | 8.2 | 0.0 | 71.3 | 25.1 | 8.26 |
| 1680 | 53SP43NS4BI | C | LT1957, LT1964 | 112 | 0 | 9.8 | 0.0 | 53.8 | 27.9 | 8.16 |
| 1681 | 83SP13NS | C | LT1957, LT1964 | 32 | 0 | 9.4 | 0.0 | 103.7 | 26.3 | 6.00 |

| No | Composition | Natura assessment | Management history | No of large trees ($ha^{-1}$) | No of large dead trees ($ha^{-1}$) | Share of dead trees (%) | Share of clumped dead trees (%) | Volume of lying deadwood ($m^3$ $ha^{-1}$) | Share of irregularly positioning trees (%) | SCI |
|---|---|---|---|---|---|---|---|---|---|---|
| 1682 | 57NS21SP16BI6NM | C | LT1957, LT1964 | 56 | 8 | 5.4 | 0.0 | 143.9 | 28.6 | 6.21 |
| 1683 | 67SP22NS10BI1BA | C | LT1957, LT1964 | 40 | 0 | 12.1 | 0.0 | 48.7 | 26.8 | 6.10 |
| 1684 | 50NS36SP14BI | B | S1974 | 32 | 0 | 10.5 | 0.0 | 5.3 | 30.6 | 7.98 |
| 1685 | 62SP29NS8BI1BA | B | S1974 | 56 | 0 | 8.3 | 0.0 | 6.1 | 18.8 | 7.62 |
| 1686 | 98NS2BI | B | S1974 | 119 | 0 | 11.3 | 0.0 | 52.3 | 18.2 | 6.66 |
| 1687 | 54SP28NS18BI | B | S1974 | 32 | 8 | 5.4 | 0.0 | 5.5 | 27.3 | 7.46 |
| 1688 | 88NS9BI3SP | B | S1974 | 48 | 24 | 9.9 | 0.0 | 83.9 | 23.5 | 6.45 |
| 1689 | 64NS20BI10SP6BA | B | S1974 | 104 | 0 | 17.6 | 0.0 | 36.0 | 21.4 | 7.89 |
| 1690 | 72NS20CA8BI | B | S1974 | 113 | 14 | 14.5 | 0.0 | 59.8 | 21.8 | 7.16 |
| 1691 | 69NS31CA | B | S1974 | 151 | 72 | 17.3 | 0.0 | 96.8 | 22.8 | 9.40 |
| 1692 | 75NS20SP5BI | B | S1974 | 85 | 0 | 14.8 | 0.0 | 22.4 | 30.4 | 6.07 |
| 1693 | 100NS | B | S1974 | 127 | 0 | 6.6 | 0.0 | 13.1 | 22.0 | 6.97 |
| 1694 | 91NS6BI3SP | B | S1974, S1985, S1993 | 56 | 8 | 8.1 | 0.0 | 81.1 | 24.6 | 6.58 |
| 1695 | 64NS15CA14BA-6BI1EA | B | S1974, S1985, S1993 | 104 | 16 | 4.8 | 0.0 | 96.9 | 31.9 | 7.69 |
| 1696 | 37NS29SP28CA6BI | B | S1974, S1985, S1993 | 40 | 16 | 8.1 | 0.0 | 11.8 | 30.4 | 7.94 |
| 1697 | 77NS19BI4BA | B | S1974, S1985, S1993 | 48 | 0 | 4.2 | 0.0 | 54.4 | 22.1 | 5.86 |
| 1698 | 74NS24CA2BI | B | S1974, S1985, S1993 | 48 | 0 | 11.3 | 0.0 | 77.7 | 28.9 | 6.37 |
| 1699 | 83NS13BI4BA | B | S1974, S1985, S1993 | 96 | 16 | 3.3 | 0.0 | 66.2 | 25.7 | 8.27 |
| 1800 | 72NS14BI7BA7CA | B | S1974, S1985, S1993 | 113 | 14 | 11.9 | 0.0 | 45.6 | 24.6 | 9.74 |
| 1801 | 82NS12BI6CA | B | S1974, S1985, S1993 | 143 | 0 | 8.9 | 0.0 | 75.9 | 19.5 | 7.22 |
| 1802 | 67NS17CA11BI5BA | B | S1974, S1985, S1993 | 40 | 8 | 4.7 | 0.0 | 25.5 | 27.0 | 7.48 |
| 1803 | 92NS7CA1BI | B | S1974, S1985, S1993 | 96 | 8 | 4.8 | 0.0 | 90.4 | 25.0 | 7.57 |
| 1804 | 57NS24SP17CA2BI | C | LT1972, S1985 | 24 | 8 | 22.1 | 9.4 | 28.8 | 22.1 | 7.34 |
| 1805 | 61SP26NS13BI | C | T1976 | 40 | 0 | 1.3 | 0.0 | 7.6 | 22.7 | 5.72 |
| 1806 | 34NS32SP28BI6CA | C | T1976 | 32 | 0 | 6.0 | 0.0 | 2.1 | 23.8 | 5.42 |
| 1807 | 78CA16NS4SP2BI | C | T1976 | 40 | 0 | 11.6 | 0.0 | 3.2 | 20.2 | 6.97 |
| 1808 | 70NS16SP10CA4BI | C | T1976 | 0 | 0 | 12.7 | 0.0 | 3.3 | 23.6 | 7.51 |
| 1809 | 47CA28NS23SP2BI | C | T1976 | 40 | 0 | 16.5 | 0.0 | 2.7 | 27.9 | 6.89 |
| 1810 | 42CA30BI18NS10SP | C | T1976 | 28 | 14 | 8.1 | 0.0 | 2.0 | 22.4 | 5.30 |
| 1811 | 67SP29NS4BI | C | T1976 | 48 | 0 | 1.5 | 0.0 | 3.2 | 23.4 | 5.62 |
| 1812 | 37SP33NS30BI | C | T1976 | 8 | 0 | 1.2 | 0.0 | 4.5 | 27.7 | 6.19 |
| 1813 | 73NS15CA8BI4SP | C | LT1972, S1985 | 56 | 16 | 8.4 | 0.0 | 20.9 | 25.7 | 7.02 |

## Appendix 2

### Species inventory methodology and results

| | |
|---|---|
| Vascular plants and bryophytes | |
| Survey methodology | Ground vegetation was surveyed between May and August 2015 across all 100 plots using a 400-m$^2$ subplot within each plot. The pin-point method (Kent & Coker, 1992) was used to estimate species coverage<br>Taxonomy: Bryophyte identification followed Ingerpuu et al. (1998), while vascular plant taxonomy was based on Leht (2010)<br>Sampling procedure: Pin-point sampling involved systematically placing metal rods (1 m in length, diameter 1.5–3.0 mm) at 1-m intervals along 20-m-long transects arranged east–west within the subplot. Each species touching the rod was recorded<br>Specimen processing: Unidentified plant and bryophyte specimens were collected, dried, and later identified and preserved at the Estonian University of Life Sciences |
| Results | Vascular plants: The inventory recorded an average of 82 (sd ± 34) vascular plant cover per plot. The minimum and maximum values observed were 9 and 159, respectively. In terms of species richness, the plots contained an average of 28 (sd ± 12) species, with a minimum of eight species and a maximum of 62 species per plot<br>Bryophytes: The inventory recorded an average of 45 (sd ± 17) bryophyte cover per plot. The minimum and maximum values observed were 7 and 86, respectively. In terms of species richness, the plots contained an average of 20 (sd ± 7) species, with a minimum of seven species and a maximum of 36 species per plot |
| Lichens and polypore fungi | |
| Survey methodology | Lichens and wood-inhabiting fungi were surveyed in 50 plots (every second plot)<br>Substrate selection: Surveys were conducted on various host materials, including canopy trees, co-dominant trees, standing dead trees (snags), fallen logs, stumps, root-mounds<br>Survey timing: Lichens were recorded from May to August 2015. Polypore fungi were surveyed from July to November 2015<br>Sampling approach: Species were documented on each selected substrate, with abundance classified using a four-level scale: 1 — very few (1–2 specimens, covering < 5% of the surface for lichens; a single fruiting body or small cluster for fungi); 2 — few (up to 10 specimens, covering 5–20% for lichens; 2–3 specimens for fungi); 3 — moderately abundant (covering 20–50% for lichens; scattered occurrence for fungi); 4 — highly abundant (covering > 50% for lichens; abundant for fungi)<br>Specimen processing: Unidentified lichen specimens were collected, dried, and later identified in the laboratory of the University of Tartu. Polypore fungi were identified in the field by a species expert |
| Results | Lichens: Lichens were recorded on 437 monitoring objects, including 257 living trees and 179 deadwood structures (snags, logs, stumps, root-mounds). The most frequent substrates were living pines (99 trees) and spruces (88 trees). The inventory recorded an average of 143 (sd ± 74) lichen specimens per plot. The minimum and maximum values observed were 23 and 181 specimens, respectively. In terms of species richness, the plots contained an average of 40 (sd ± 28) species, with a minimum of six species and a maximum of 59 species per plot<br>Polypore fungi: All wood-inhabiting polypore fungi found within each plot were recorded, including their host substrate. The inventory recorded an average of 15 (sd ± 8) polypore fungi specimens per plot. The minimum and maximum values observed were three and 38 specimens, respectively. In terms of species richness, the plots contained an average of 6 (sd ± 2) species, with a minimum of two species and a maximum of 12 species per plot |
| Beetles (*Coleoptera*) | |
| Survey methodology | Sampling method: Flight-intercept traps (window traps) were used to collect beetles. A total of 10 traps were deployed, with one per every 10 sample plots. Traps were attached to dead trees or stumps at 1.3-m height using a metal rod. Each trap consisted of a transparent plastic panel (55 × 45 cm) with a collecting container (55 × 15–20 cm, depth 13 cm) filled with preservative fluid. A polyethylene roof (60 × 60 cm) protected traps from rain and debris. Traps were checked every 2 weeks from May to August 2015, for a total of eight collection events. Specimens were preserved in ethanol, counted, and identified in the laboratory<br>Beetle species identification followed Silfverberg (2010). Collected beetles, including unidentified specimens, were preserved at the Estonian University of Life Sciences and in the Ilmar Süda private collection |
| Results | The inventory recorded an average of 133 (sd ± 9) beetle species per plot. The minimum and maximum values observed were 117 and 148 species, respectively. In terms of specimen abundance, the plots contained an average of 3250 (sd ± 1445) individuals. The minimum number of beetles found in a plot was 1350, while the maximum was 6425 |

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