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Variation in Deadwood Microsites in Areas Designated under the Habitats Directive (Natura 2000)

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Abstract: The continuing decline in biodiversity presents a major environmental protection challenge. The conservation of sufficiently extensive and diverse habitats requires an array of coordinated actions, often involving large areas. While a set of conservation objectives have been defined for the Natura 2000 network, no universal methods of accomplishing them have been specified, and so they must be designed by individual Member States. Deadwood volume and the density of large deadwood pieces are widely used for evaluating the quality of forest habitat types designated under the Habitats Directive. In the present study, data from 5557 sample plots were used to evaluate the mean values of the two deadwood indicators as well as the ratio of deadwood volume to living tree volume for each of the 13 habitat types in Poland. In addition, a logistic regression model was constructed to evaluate the effects of terrain, site, and tree stand characteristics as well as protection type on deadwood volume in Natura 2000 areas. Mean deadwood volume varied greatly between habitat types, with the lowest values found for Central European lichen Scots pine forests (91T0–2.5 m^3 ha^{-1}) and Old acidophilous oak woods (9190–4.4 m^3 ha^{-1}), and the highest for Riparian mixed forests (91F0–43.1 m^3 ha^{-1}) and Acidophilous *Picea* forests of the montane to alpine levels (9410–55.4 m^3 ha^{-1}). The ratio of deadwood volume to living tree volume ranged from approx. 1%–17%. Additionally, the presence of large deadwood differed among habitat types: in some, there were no deadwood pieces with a diameter of ≥50 cm, while their maximum density was 6.1 pieces ha^{-1}. The logistic regression model showed that the likelihood of a habitat type to have a 'favorable conservation status' as defined by deadwood abundance (a threshold of at least 20 m^3 ha^{-1} according to Polish manuals on habitat type evaluation) increased with sample plot elevation, site fertility, and moisture, as well as stand age and volume. Positive effects were also observed for forests under strict and active protection versus managed forests. Planned efforts are necessary to enhance the quality of habitats with insufficient deadwood, especially in managed forests. Special attention should be given to areas that are readily accessible due to gentle terrain and low site moisture. Furthermore, younger stands on less fertile sites may require intervention to promote deadwood accumulation. We recommend retaining a certain proportion of mature stands until natural death and decomposition. Increasing the density of large deadwood is currently one of the most pressing conservation needs in most habitat types.

Keywords: reserve network; biodiversity; large trees; snags; coarse woody debris; regression model; habitat conditions; strict protection; managed forests

1. Introduction

Europe boasts the largest network of coordinated conservation areas in the world, known as Natura 2000, which covers more than 18% of the land area of EU Member States and almost 10%

of their territorial waters. Its overarching objective is to ensure long-term conservation of valuable and endangered species and habitats [1–5] in line with the EU legislation including the 1979 Birds Directive [6] and the 1992 Habitats Directive [7]. As far as the habitat types defined under the latter directive are concerned, this means that their range should be preserved (and possibly expanded) and that they should retain their specific structure, functions, as well as characteristic species. The Natura 2000 network extends protection to a total of 231 habitat types; the greatest number of which are forest habitats (81), accounting for half of the entire Natura 2000 area [8]. The EU's special interest in forests is attributable to the fact that natural and semi-natural woodlands are among the most biologically diverse ecosystems on Earth. Although more than 1/3 of Europe is covered with forests, only 10% of their area consists of natural or semi-natural stands that significantly contribute to preserving plant and animal species [4]. While the Habitats Directive [7] laid out a number of conservation goals, it did not indicate specific ways of achieving them, with each Member States being responsible for developing its own solutions [9].

The Habitats Directive [7] requires the countries participating in the Natura 2000 network to monitor the conservation status of the natural habitats and species listed in its appendixes. The monitoring of forest sites encompasses a number of elements, such as their range, area, the species composition of all forest layers, species provenance, the age and vertical structure of vegetation, as well as soil and water conditions. It is essential to identify the factors and threats affecting a given habitat type, such as those associated with forest management [10], which could deteriorate habitat quality and decrease biodiversity. In this context, of importance is a sufficient presence of diverse microsites offered by so-called biocenotic trees, large trees, and dead trees [11,12]. Importantly, as many as 25% of species found in forests are facultatively or obligately associated with deadwood, and some of them are among the most endangered organisms of European temperate forest ecosystems [13]. Their presence is dependent not only on the quantity, but also the quality of deadwood, such as species, diameter, and decay stage [14,15]. Therefore, the removal of dead and dying trees is perceived as detrimental to most forest habitats and is being monitored on Natura 2000 sites [10]. The adoption of an appropriate deadwood management strategy requires knowledge about the ecology of saproxylic organisms, including the size and dispersal of their populations. Such information is needed to decide whether deadwood volume should be increased evenly across the entire managed forest area, but only to a limited extent, or perhaps the focus should be on a substantial improvement in the number and diversity of deadwood microsites in selected areas [16]. Investigations aiming to determine deadwood thresholds have indicated a wide range of desirable deadwood volumes [17]. Threshold values for different habitat types are also provided in guidelines for assessing Natura 2000 sites [18,19].

Currently, in Poland there are 849 special areas of conservation (SACs) with an overall area of 3.9 million ha. They represent 77 habitat types listed in Annex I to the Habitats Directive. Seventeen of them are priority habitat types, whose range is mostly or exclusively limited to the territory of the EU Member States, and so their survival depends directly on the conservation efforts undertaken by those countries. The natural habitat types identified under the Habitats Directive are classified into aquatic and waterside, heath and scrub, meadow, grassland, boggy, rocky, as well as typical forest categories [20]. This work focuses on forest habitats, and in particular on the deadwood they contain as a factor strongly affecting biodiversity. The study involved data derived from several thousand sample plots located on 312 Natura 2000 sites distributed throughout Polish lowlands, uplands, and mountains. Deadwood volume and the density of large deadwood pieces were analyzed with respect to guidelines specifying their threshold values in habitats. Logistic regression was used to determine which site, stand, and protection parameters had a significant effect on deadwood accumulation in those habitats. The results could be helpful in designing appropriate actions and strategies to improve habitat quality.

2. Materials and Methods

2.1. Data Collection

As part of the National Forest Inventory (NFI), Poland is covered with a 4 × 4 km grid of sample plots based on the 16 × 16 km ICP Forests network used in the European Union to evaluate forest damage [21]. At each node, there is an L-shaped cluster of five sample plots spaced 200 m apart (Figure 1). The exact rules for taking measurements and general reports on forest conditions are presented in ME [22] and NFI [23]. Depending on the age of the dominant tree species, the sample plots range in size from 200 to 500 m^2. In the present study, diameter at breast height (DBH) was measured for standing living and dead trees, while in the case of snags (with a height of at least 0.4 m) and downed deadwood, diameter was measured halfway along their height or length, respectively. Only standing trees with a DBH of >7 cm and downed deadwood fragments with a diameter of >10 cm at the thicker end were included in the study. Measurements were conducted for those dead trees or their fragments that grew within the sample plots prior to death. Thus, the entire length of deadwood fragments lying across sample plot borders was included. On the other hand, stumps left from management procedures were excluded.

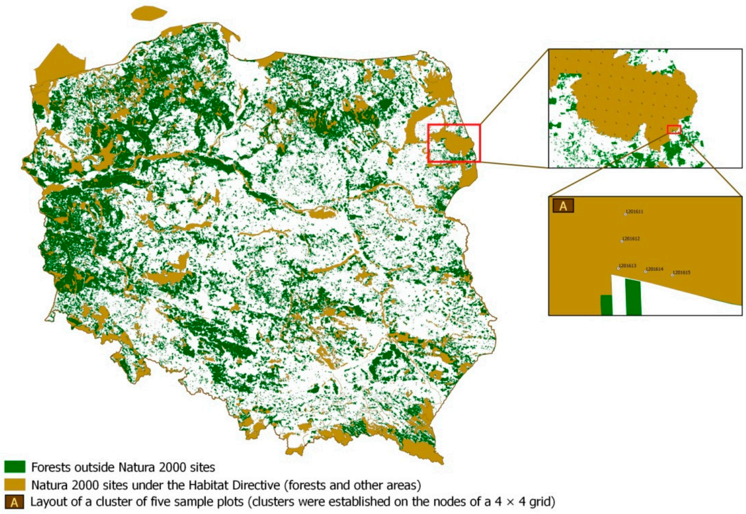

Figure 1. Sites designated under the Habitats Directive and the layout of a cluster of sample plots.

Forest ecosystems were evaluated on the basis of data obtained in the years 2010–2014 from NFI sample plots located within Natura 2000 sites under the Habitat Directive, also known as special areas of conservation (SACs). NFI measurements were conducted only for plots located on sites classified as forest areas pursuant to Polish regulations. In the study period each sample plot was measured once [23]. To determine which sample plots should be included in the study, the authors used a spatial dataset in the form of ESRI Shapefile layers including:

- vector data for the location of NFI sample plots;
- SAC database containing vector and descriptive data concerning forms of nature conservation [24]; and
- vector and descriptive data for tree stands from the Forest Data Bank [25].

These input data were integrated using Qgis 2.14 software to ensure information compatibility and generate an information layer for tree stands and sample plots within the boundaries of Natura 2000 sites. As a result, 312 Natura 2000 sites (SACs) with an overall area of 3,102,247 ha, and with a total of 5557 NFI sample plots located on them, were available for the study. Those SACs included the habitat types listed in Annex I and the habitats of species listed in Annex II. The next step involved the identification of the location and type of the various Natura 2000 habitats on the aforementioned

SACs [7], as well as the NFI sample plots within their boundaries. For that purpose, we used Standard Data Forms providing information about the habitat types present on a given site, as well as conservation plans (or drafts of those plans) specifying their location. For Natura 2000 sites without protection plans, natural habitats were identified using methodological keys based on taxonomical descriptions of tree stands [26], as well as the available literature, naturalists' notes, and manuscripts concerning a given Natura 2000 site. In total, the 312 selected Natura 2000 SACs were found to contain 15 habitat types (including four priority types) with a total area of 711,306 ha. While 1620 NFI sample plots were located within the boundaries of 14 of those habitat types (see Table 1), as many as 3937 sample plots present in Natura 2000 SACs were found in habitats not listed in Annex I to the Habitat Directive [7]; in this work the latter were designated as "no habitat type" (NHT).

Table 1. Habitats Directive forest types and the number of plots sampled.

Annex I Code	Habitat Type	Number of Sample Plots
9110	*Luzulo-Fagetum beech* forests	133
9130	*Asperulo-Fagetum beech* forests	566
9140 [1]	Medio-European subalpine beech woods with *Acer* and *Rumex arifolius*	4
9160	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the *Carpinion betuli*	52
9170	*Galio-Carpinetum* oak-hornbeam forests	399
9180 *	*Tilio-Acerion* forests of slopes, screes and ravines	10
9190	Old acidophilous oak woods with *Quercus robur* on sandy plains	31
9410	Acidophilous *Picea* forests of the montane to alpine levels (*Vaccinio-Piceetea*)	58
9420	Alpine *Larix decidua* and/or *Pinus cembra* forests	0
91D0 *	Bog woodland	143
91E0 *	Alluvial forests with *Alnus glutinosa* and Fraxinus excelsior (*Alno-Padion, Alnion incanae, Salicion albae*)	132
91F0	Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)	49
91I0 *	Euro-Siberian steppic woods with *Quercus* spp.	7
91P0	Holy Cross fir forest (*Abietetum polonicum*)	13
91T0	Central European lichen Scots pine forests	23

[1] Habitat type 9140 was excluded from comparative habitat analyses due to the small number of plots. * Priority habitat types.

In addition, the Web Map Service made available by the Main Office for Surveying and Cartography was used with the C-GEO software package (with web connection) to assess elevation above sea level for each sample plot. Elevation was determined in accordance with the Polish system PL-KRON86-NH by means of interpolation algorithms prepared on the basis of the Numerical Terrain Model with a 1×1 m grid.

The criteria concerning deadwood volume and the density of large deadwood may differ depending on the specific characteristics of a given habitat. Those criteria are specified in manuals on habitat evaluation in Poland [10,27]. In most cases, a favorable conservation status requires a deadwood volume of >20 m^3 ha^{-1} and a density of at least 3–5 large deadwood pieces per ha; large pieces are understood as those having a diameter/DBH of >50 cm (or in some cases >30 cm) and a length/height of >3 m (Table 2). Medium-sized trees are defined as those with a diameter/DBH in the range of 30–49.9 cm, and large trees as those with a DBH of ≥ 50 cm.

In some cases, the deadwood volume threshold in a given habitat may be expressed as a proportion of stand volume rather than in absolute values. Furthermore, in some habitat types, such as 91T0, the presence of deadwood is generally undesirable given the adopted conservation priorities. This is due to the fact that large amounts of deadwood on the forest floor lead to rapid enrichment of the substrate in biogenic substances, thus increasing the competition of bryophytes and herbaceous plants to the detriment of terricolous lichens. While small amounts of deadwood are not harmful, large quantities of twigs and branches left, e.g., in the aftermath of management procedures, may cause habitat degradation [27].

2.2. Data Analysis

Data from sample plots were used to determine the mean deadwood volume for the studied habitat types. The volume of living trees and the proportion of deadwood volume to living tree volume were assessed for each habitat type to account for variation in site productivity. Then, the density and variability of medium-sized and large deadwood pieces were evaluated. Due to NFI methodology and the definition of medium-sized and large deadwood pieces (Table 2), the diameter of logs at the thicker end was calculated based on measurements taken halfway along their length (adopting a mean taper of 1 cm per 1 m). Statistical differences between habitat types were evaluated by analysis of variance and the Kruskal–Wallis test implemented in Statistica 13 software (StatSoft, Kraków, Poland).

The factors affecting deadwood volume in the studied habitat types were evaluated using a logistic regression model [28]. The choice of that statistical tool was dictated by the uneven distribution of deadwood, whose volume varied greatly among sample plots and which was absent from approx. half of them. The logistic regression model used a dichotomous dependent variable [28]. Sample plots with a deadwood volume of >20 m^3 ha^{-1} were assigned the value of 1, with 0 assigned to other plots. The 20 m^3 ha^{-1} threshold corresponds to the favorable conservation status as defined for most of Natura 2000 habitat types. The adopted independent variables were factors that may affect deadwood volume, such as stand, terrain, and site characteristics, as well as protection type, also obtained from the NFI. The protection type variable assumed three values: active, strict, or managed forest. For the purposes of this work, 'managed forests' are defined as forest areas that are managed with no active or strict protection plans. In turn, active and strict protection plans are most often used in nature reserves and national parks. Terrain was described by two variables: elevation above sea level (m a.s.l.) and the percentage slope of sample plots (%). Tree stands were characterized by the age of the dominant tree species (years), the volume of living trees (m^3 ha^{-1}), and tree density (trees ha^{-1}). The model also included site fertility (dystrophic, oligotrophic, mesotrophic, eutrophic) and moisture (mesic, moist, boggy), as those parameters varied considerably among the studied habitat types. Another independent variable was habitat type, operationalized by assigning one of 13 Natura 2000 habitat codes, or "no habitat type" (NHT) for sample plots in habitats not included in Natura 2000.

Table 2. Deadwood volume and density indicators for the various habitat types [10,27,29,30].

Habitat Types	Parameter/Indicator					
	Deadwood (Overall Volume)			Standing or Downed Deadwood ≥3 m Long and ≥50 cm in Diameter [1]		
	Conservation Status of the Habitat					
	Favorable FV	Unfavorable–Inadequate U1	Unfavorable–Bad U2	Favorable FV	Unfavorable–Inadequate U1	Unfavorable–Bad U2
	(m^3 ha^{-1})			(pieces ha^{-1})		
9110	>20	10–20	<10	>5	3–5	<3
9130	>20	10–20	<10	>5	3–5	<3
9140	d.n.a. [5]	d.n.a.	d.n.a.	d.n.a.	d.n.a.	d.n.a.
9160	>20	10–20	<10	>5	3–5	<3
9170	>20	10–20	<10	>5	3–5	<3
9180	d.n.a.	d.n.a.	d.n.a.	d.n.a.	d.n.a.	d.n.a.
9190	>20	10–20	<10	>5	3–5	<3
9410	>20	10–20	<10	>5	3–5	<3
91D0	d.n.a.	d.n.a.	d.n.a.	>3 [2]	1–3 [2]	<1 [2]
91E0	>20	10–20	<10	>5 [1]	3–5 [1]	<3 [1]
91F0	>20	10–20	<10	>5	3–5	<3
91I0	<5% [3]	5–20% [3]	> 50% [3]	d.n.a.	d.n.a.	d.n.a.
91P0	>10% [4]	3–10% [4]	<3% [4]	d.n.a.	d.n.a.	d.n.a.
91T0	None	A small amount due to natural processes	Large amount, e.g., heaps of branches	d.n.a.	d.n.a.	d.n.a.

[1] The diameter threshold was lowered to 30 cm in habitats where trees do not normally reach 50 cm for natural reasons. Those values represent diameter at breast height (DBH) for standing trees and either DBH (if measurable) or diameter at the thicker end for downed deadwood. [2] Diameter threshold lowered to 30 cm. [3] This value refers exclusively to downed deadwood in relation to stand volume, e.g., <5% means that downed deadwood volume amounts to less than 5% of stand volume. [4] In relation to stand volume. [5] d.n.a.—not available.

The model was built using the step-wise forward method (a model constructed using the step-wise backward method arrived at the same set of significant variables). The odds ratio was calculated to characterize the effects of independent variables on the dependent variable. In the case of quantitative independent variables, an increase or decrease by one unit increased or decreased the probability for the dependent variable to assume the value of 1 by the odds ratio. In the case of qualitative variables, the odds ratio was adopted in the form of reference values for each of them. The independent variables were tested for intercorrelations. The quality of the model was evaluated by means of Nagelkerke values and the Hosmer–Lemeshow test [31]. A successful classification test was carried out on the basis of observations used to estimate the parameters of the model [32].

3. Results

The mean deadwood volume for the entire Natura 2000 area was 12.7 m^3 ha^{-1}, with very large differences between habitat types (Kruskal–Wallis H = 235.7; $p < 0.05$). The lowest deadwood volume was found for Central European lichen Scots pine forests (91TO–2.5 m^3 ha^{-1}) and Old acidophilous oak woods (9190–4.4 m^3 ha^{-1}), and the highest for Riparian mixed forests (91F0–43.1 m^3 ha^{-1}) and Acidophilous *Picea* forests of the montane to alpine levels (9410–55.4 m^3 ha^{-1}). Furthermore, substantial variation was recorded for sample plots located within one habitat type, as reflected by very high standard error values (Table 3).

Table 3. Mean deadwood and living tree volumes and their ratio for individual habitat types.

Habitat Type	Deadwood Volume (Standard Error) (m^3 ha^{-1}) *	Living Trees Volume (Standard Error) (m^3 ha^{-1}) *	Deadwood Volume to Living Trees Volume Ratio (%)
9110	13.9 (2.9) bc	373 (18.8) BD	3.7
9130	28.4 (2.3) a	434 (10.4) B	6.5
9160	21.5 (9.3) c	478 (38.2) BE	4.5
9170	9.3 (1.5) c	327 (9.2) D	2.8
9180	25.2 (12.0) ac	439 (79.8) ABD	5.8
9190	4.4 (2.1) c	407 (45.9) BCD	1.1
9410	55.4 (13.4) a	326 (32.6) ADE	17.0
91D0	8.6 (1.5) bc	238 (14.9) A	3.6
91E0	25.1 (3.7) ab	335 (16.3) CDE	7.5
91F0	43.1 (12.5) ac	378 (36.0) BCD	11.4
91I0	7.9 (6.7) ac	335 (63.9) ABD	2.4
91P0	15.4 (9.9) ac	306 (50.8) ABD	5.0
91T0	2.5 (1.2) c	282 (26.7) ABD	0.9
NHT	9.4 (0.5) c	279 (2.9) AC	3.4

* values with different letters differ significantly at $p < 0.05$ as evaluated by the nonparametric Kruskal–Wallis test with a post hoc correction for the number of comparisons).

The mean volume of living trees for the entire Natura 2000 area was 305 m^3 ha^{-1}. Among the habitat types, the lowest values were found for bog woodland (91D0–238 m^3 ha^{-1}) and Central European lichen Scots pine forests (91T0–282 m^3 ha^{-1}). Volumes in the range of 300–400 m^3 ha^{-1} were recorded for seven habitat types, with the highest value for Sub-Atlantic and medio-European oak or oak-hornbeam forests of the *Carpinion betuli* (9160–478 m^3 ha^{-1}), with differences between habitats often reaching statistical significance (Kruskal–Wallis H = 301.7; $p < 0.05$, see Table 3). The ratio of deadwood volume to stand volume ranged from approx. 1% in 91TO and 9190 to 11.4% in 91F0 and 17.0% in 9410 (Table 3).

Medium-sized and large living trees (DBH ≥30 cm) were found in all habitat types, ranging from 94 trees ha^{-1} in 91D0 to 164 trees ha^{-1} in 91I0, with a mean value of 121 trees ha^{-1} (Kruskal–Wallis H = 147.3; $p < 0.05$) (Figure 2). Medium-sized and large deadwood was not found in Euro-Siberian steppic woods with *Quercus* spp. (91I0) and in Central European lichen Scots pine forests (91T0). In the other habitat types its mean density ranged from 2.5 pieces ha^{-1} (9190) and 2.7 pieces ha^{-1} (91D0) to 16.3 pieces ha^{-1} (9130) and 31.1 pieces ha^{-1} (9410) (Figure 3). Differences were also found when analyzing the density of large living trees only (DBH of ≥50 cm, Kruskal–Wallis H = 878.1; $p < 0.05$), which ranged from 4 trees ha^{-1} for 91T0 to 61 trees ha^{-1} for 9180, with a mean of 16 trees ha^{-1} (Figure 2). Large deadwood pieces were absent in a total of five habitat types. In the other habitat types their mean density ranged from 0.4 pieces ha^{-1} (9170) and 0.8 pieces ha^{-1} (91E0) to 5.6 pieces ha^{-1} (91F0) and 6.1 pieces ha^{-1} (9410) (Figure 3).

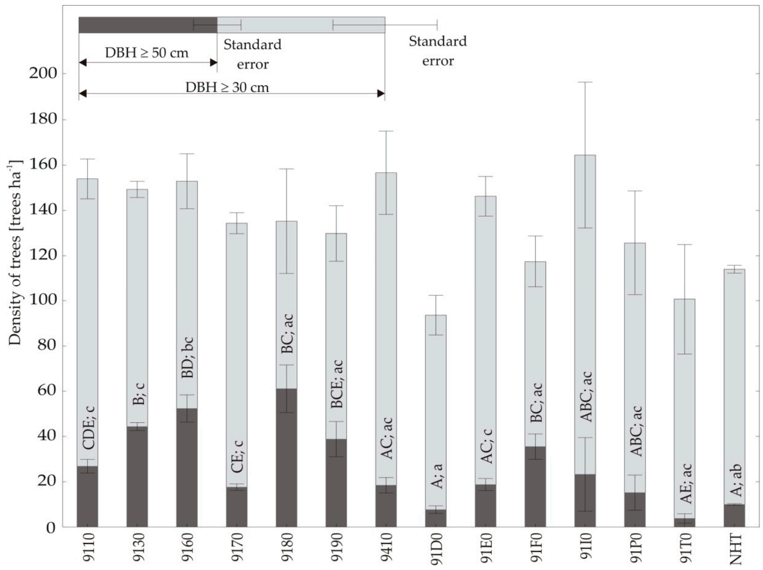

Figure 2. Density of medium-sized and large living trees. Values with different letters differ significantly at $p < 0.05$ as evaluated by the nonparametric Kruskal–Wallis test with a post hoc correction for the number of comparisons. Uppercase letters refer only to trees with DBH ≥ 50 cm while lowercase letters refer to all trees with DBH ≥ 30 cm. Note: DBH–diameter at breast height.

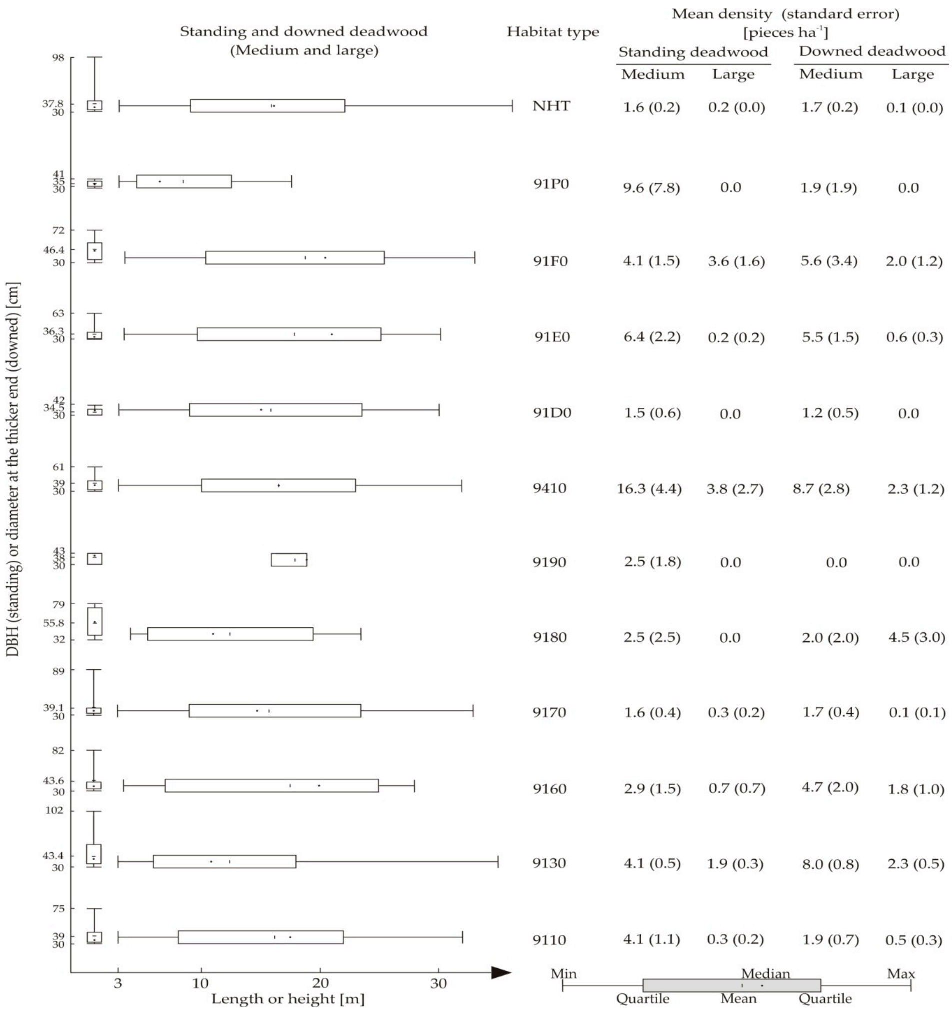

Figure 3. Characteristics of medium-sized and large deadwood in the various habitat types.

The inclusion of factors other than habitat type in the analysis (Table 4) substantially changes the picture of deadwood accumulation compared to analysis based exclusively on habitat types (Table 3). The logistic regression model indicates that deadwood volume is mostly determined by factors associated with terrain and site accessibility, type of protection, as well as soil and stand parameters (Table 4). From among the nine variables entered in the model, the slope of sample plots and living tree density failed to reach statistical significance, while elevation above sea level, protection type, site fertility and moisture (water abundance), the age of the dominant tree species, and the volume of living trees were significant. An increase in the quantitative variables (elevation, stand age, living tree volume) was associated with an increase in the odds ratio, or the likelihood of finding a favorable deadwood volume (>20 m^3 ha^{-1}) in a given habitat type. In terms of site conditions, the reference value corresponded to sites poorest in nutrients. The odds ratio increased with both site fertility and moisture; in the latter case the highest odds ratio was recorded for boggy sites. There was a substantial difference in the odds ratio between managed forests and areas subjected to either active or strict protection. A significant effect was also found for habitat type, which was the last element entered into the model. No habitat type exhibited a significant difference as compared to the reference value in the model (Central European lichen Scots pine forests–91T0).

Table 4. Logistic analysis results for the likelihood of a sample plot exhibiting a deadwood volume greater than 20 m^3 ha^{-1} (the threshold value for a favorable conservation status in most habit types).

Independent Variable [1]	β (Standard Error)	Wald's Chi-Square	Odds Ratio (95% Confidence Interval)	p *
Elevation (m a.s.l.)	0.003 (0.000)	328.052	1.003 (1.003–1.004)	<0.001
Age (year)	0.008 (0.001)	33.569	1.008 (1.006–1.011)	<0.001
Living trees volume (m^3 ha^{-1})	0.001 (0.000)	7.108	1.001 (1.000–1.001)	0.008
Protection (management) type		73.002		<0.001
Managed forests	Reference			
Active protection	0.860 (0.111)	60.058	2.363 (1.901–2.937)	<0.001
Strict protection	0.865 (0.185)	21.948	2.376 (1.654–3.413)	<0.001
Fertility		46.342		<0.001
DYSTROPHIC	Reference			
OLIGOTROPHIC	0.623 (0.224)	7.721	1.864 (1.201–2.893)	0.005
MESOTROPHIC	0.924 (0.212)	18.902	2.519 (1.661–3.820)	<0.001
EUTROPHIC	1.261 (0.212)	35.368	3.528 (2.328–5.345)	<0.001
Moisture		65.228		<0.001
MESIC	Reference			
MOIST	0.657 (0.132)	24.649	1.929 (1.488–2.501)	<0.001
BOGGY	1.320 (0.178)	55.167	3.742 (2.641–5.300)	<0.001
Habitat type		27.431		0.011
91T0	Reference			
9110	−0.760 (1.084)	0.492	0.467 (0.056–3.911)	0.483
9130	−0.526 (1.061)	0.246	0.591 (0.074–4.728)	0.620
9160	0.187 (1.126)	0.028	1.206 (0.133–10.962)	0.868
9170	−0.077 (1.065)	0.005	0.926 (0.115–7.463)	0.943
9180	0.232 (1.277)	0.033	1.261 (0.103–15.416)	0.856
9190	−1.817 (1.468)	1.533	0.163 (0.009–2.885)	0.216
9410	−0.308 (1.095)	0.079	0.735 (0.086–6.292)	0.779
91D0	−0.237 (1.088)	0.047	0.789 (0.094–6.661)	0.828
91E0	0.381 (1.077)	0.125	1.464 (0.177–12.089)	0.723
91F0	0.325 (1.111)	0.086	1.385 (0.157–12.223)	0.770
91I0	−1.025 (1.552)	0.436	0.359 (0.017–7.514)	0.509
91P0	−0.568 (1.338)	0.180	0.567 (0.041–7.802)	0.671
NHT	−0.066 (1.053)	0.004	0.936 (0.119–7.366)	0.950
Constant term	−4.721 (1.041)	20.574	0.009 (0.001–0.069)	<0.001

Quality characteristics of the model: Likelihood-ratio test: $\chi^2 = 939.5$; $p < 0.0001$; Nagelkerke's coefficient $R^2 = 0.272$. The model correctly predicted results in 85% of the cases (44% for 1 and 92% for 0); the Hosmer–Lemeshow test = 13.4; $p = 0.10$. * All the p-values are from Wald's tests.

4. Discussion and Conclusions

It is crucial to develop appropriate strategies for Natura 2000 sites to aid policymakers and managers in reaching biodiversity targets [33,34]. Despite an increase in Europe's afforestation, it is estimated that only 15% of its woodland qualifies for a favorable conservation status [35]. The study provides a general overview of the conservation status of forest habitats in Poland. The use of a large number of sample plots made it possible to determine mean values for 13 habitat types. However, it should be noted that the status of a given habitat type may vary between different SACs. The statistical method applied by the NFI, employing a random, evenly distributed network of sample plots, precludes the evaluation of individual SACs due to an insufficient number of representative sample plots in each of them. Nevertheless, it is an excellent, objective tool providing a general characterization of Natura 2000 sites. In addition, logistic regression analysis revealed the site and stand characteristics that have a positive or negative effect on deadwood accumulation in areas designated under the Habitats Directive. Knowing the characteristics of individual SACs and the factors conducive to deadwood accumulation, one can predict deadwood volume for the various areas.

In Poland, deadwood thresholds adopted for most habitat types are 20 m^3 ha^{-1} for favorable conservation status and 10–20 m^3 ha^{-1} for unfavorable-inadequate status. While this is supported by some publications, those thresholds represent the lower limits of deadwood ranges proposed for European forests. Indeed, papers on the conservation of various saproxylic species or groups of species tend to suggest thresholds of 30–50 m^3 ha^{-1}, or even more [17,36,37]. In addition to the quantitative criterion, it is also necessary to ensure variability in deadwood types [38] as well as an adequate spatial distribution of deadwood microsites [16,39]. In some cases, a deadwood volume threshold may be expressed in terms of its proportion relative to stand volume. In the present study, the deadwood volume threshold of 20 m^3 ha^{-1} amounted to only a few percent of the mean stand volume (approx. 300 m^3 ha^{-1}).

National parks and nature reserves, which are almost exclusively subjected to strict or active protection, revealed a markedly higher likelihood of reaching the threshold deadwood volume. However, the overall area of parks and reserves is relatively small (approximately 4% of the afforested area of Poland) as compared to that of managed forests. Given the well-established differences between managed and unmanaged woodland [40–42], it is little wonder that favorable volumes of deadwood as defined under Natura 2000 are usually found in the latter. In turn, in managed forests, deadwood volume mostly depends on the adopted management principles and their implementation. Taking into account the specific features of a given site, management procedures are determined by the species composition of the stand, its functions, as well as management objectives [43]. The implementation of different felling systems, management interventions, and regeneration patterns may result in significant differences in deadwood volume between sites [44–46]. In the present study, the average deadwood volume on Natura 2000 sites was 12.7 m^3 ha^{-1}, which is more than twice higher than the mean volume reported for all Polish forests (5.9 m^3 ha^{-1}, NFI 2014). This is attributable to the fact that the Natura 2000 network primarily encompasses the best preserved woodlands in the country, including protected areas. A general assessment of Natura 2000 sites (not only forests) conducted in the years 2017–2018 as part of a periodic monitoring program revealed a declining proportion of sites with a favorable status and an increase in unfavorable-inadequate and unfavorable-bad sites [47]. In the case of some forest habitats (e.g., 91F0), general conservation status deteriorated substantially due to adverse quantitative and qualitative changes in the floristic composition, the presence of alien species, as well as hydrological disturbances [47,48]. Furthermore, it has been reported that the conservation status of many sites has been affected by excessive deadwood removal; of particular concern is the scarcity of large deadwood pieces [47].

While the management difficulty indices calculated for Polish montane and lowland forests are highly varied [49], the terrain factor was found to be significant in the model, suggesting that the higher the site elevation the higher the likelihood of finding more deadwood. A large proportion of Natura 2000 woodland sites are located in mountainous areas. Habitat types that are in part or in their entirety represented by such sites and those which are otherwise associated with steep slopes (9130, 9180, 9410) exhibited higher deadwood volumes. Additionally, monitoring reports have indicated a much better quality of forest habitats in the Alpine biogeographical region as compared to the continental region. While the conservation status of mountainous sites is usually classified as favorable or unfavorable-inadequate, that of sites in the continental region is more often deemed unfavorable-inadequate or unfavorable-bad [47]. In managed forests, higher deadwood accumulation is significantly promoted by harvesting and skidding difficulty as well as by a less dense road network [50,51], entailing higher operating costs. Site accessibility also plays a role in lowland areas, but probably to a lesser extent [52].

While the mean deadwood volume varied considerably between different habitats, terrain and stand characteristics were of primary importance. The presented model indicated a significant contribution of stand age: the older the stand, the higher the likelihood of the site reaching the deadwood volume threshold. Since the Natura 2000 network has a relatively short history in Poland, the age structure of stands at the time of their inclusion continues to play a major role in habitat evaluation. Indeed, in the case of some habitat types this may partially explain the low deadwood volume and density of large dead trees. A good case in point are boggy coniferous forests, which were often represented by young stands at the time of their inclusion in Natura 2000, and so they have not had the time to accumulate enough large deadwood [27]. Nevertheless, stand structure analysis indicates quite high current mean densities of living trees with DBH ≥30 cm for all habitat types. Although boggy coniferous forests still reveal lower values, in the coming years they should add more large deadwood as long as they are appropriately managed. Moreover, although trees with DBH ≥50 cm are found in all habitat types, their distribution is much more irregular than that of medium-sized trees. This may be attributable to many factors, such as the adopted rotation period in managed forests or site conditions that determine the growth capacity of trees in individual habitat types. Large deadwood, which is particularly important for supporting biodiversity, is scarce or absent in many habitats. Since deadwood is deemed a crucial structural forest indicator [12], an improvement in that parameter is a crucial target that should be pursued with a view to enhancing the quality of Natura 2000 forest habitats.

In the present study, the habitat type with the greatest mean deadwood volume was Acidophilous *Picea* forests of the montane to alpine levels, although the high standard error points to an irregular distribution pattern with local aggregations attributable to frequent biotic and abiotic disturbances [53]. It should be noted that disturbances fulfill an important role in biodiversity promotion as long as the dying and dead trees are retained in the ecosystem, which is often the case in this habitat type due to its location in poorly accessible mountainous regions within the boundaries of Polish national parks. The diverse array of niches afforded by deadwood provide suitable microhabitats, shelter, and nutrition for a variety of species, increasing their numbers in a given area [54,55]. Other habitat types also contain trees which currently tend to exhibit high mortality, such as *Fraxinus excelsior* L., which occurs as an accompanying species in habitat types 91E0 and 91F0 [52,56].

The above notwithstanding, it should be noted that deadwood is not desirable in some habitats (91T0 and 91I0) as it may interfere with the conservation of the priority species occurring in them [27] due to the chemical properties of decomposing wood and its role in nutrient cycling and soil forming processes [57–59]. Indeed, both in 91T0 and 91I0 the mean deadwood volume is among the lowest with no medium- or large-sized deadwood despite the presence of large trees. However, a decision to protect certain species (e.g., rare lichens) by removing deadwood from a given habitat to prevent site eutrophication should be compensated on other sites as some saproxylic organisms have very specific requirements concerning deadwood type and other site conditions, such as insolation [60,61].

The applied regression model indicates that, in addition to protection type, deadwood volume is mostly influenced by terrain conditions, site fertility and moisture, stand age, and living tree volume. Analysis involving a dichotomous dependent variable for deadwood volume with a threshold value of 20 m^3 ha^{-1} shows that appropriate deadwood management should mitigate the effects of the aforementioned independent variables, or at least decrease their odds ratio. The factors that were found significant in the model were generally attributable to the "forces of nature." No sizable effects of management interventions were found for readily accessible terrain and for sites characterized by low growing stock. Thus, it is necessary to design a strategy for those habitats where deadwood is desirable and where standard management procedures and natural disturbances are insufficient to ensure favorable conservation outcomes. Particularly problematic is the scarcity of large deadwood. Therefore, in managed forests fragments of saw timber stands should be left to die naturally and decay. Further monitoring is necessary as the evaluation of the Natura 2000 network depends both on its duration in individual Member States and on the adopted conservation principles for the included areas.

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