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Long-Term Cumulative Effect of Management Decisions on Forest Structure and Biodiversity in Hemiboreal Forests

Teele Paluots [1,2,*], Jaan Liira [3], Mare Leis [4], Diana Laarmann [1], Eneli Põldveer [1], Jerry F. Franklin [5] and Henn Korjus [1]

[1] Institute of Forestry and Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia; henn.korjus@emu.ee (H.K.)
[2] Estonian State Forest Management Centre, Mõisa/3, Sagadi Village, 45403 Haljala Municipality, Estonia
[3] Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, J. Liivi tn 2, 50409 Tartu, Estonia
[4] Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Fr. R. Kreutzwaldi 5, 51006 Tartu, Estonia
[5] School of Environmental and Forest Sciences, University of Washington, Winkenwerder, Seattle, WA 98195-2100, USA
* Correspondence: teele.paluots@rmk.ee

Abstract: We evaluated the long-term impacts of various forest management practices on the structure and biodiversity of Estonian hemiboreal forests, a unique ecological transition zone between temperate and boreal forests, found primarily in regions with cold winters and moderately warm summers, such as the northern parts of Europe, Asia, and North America. The study examined 150 plots across stands of different ages (65–177 years), including commercial forests and Natura 2000 habitat 9010* "Western Taiga". These plots varied in stand origin—multi-aged (trees of varying ages) versus even-aged (uniform tree ages), management history—historical (practices before the 1990s) and recent (post-1990s practices), and conservation status—protected forests (e.g., Natura 2000 areas) and commercial forests focused on timber production. Data on forest structure, including canopy tree diameters, deadwood volumes, and species richness, were collected alongside detailed field surveys of vascular plants and bryophytes. Management histories were assessed using historical maps and records. Statistical analyses, including General Linear Mixed Models (GLMMs), Multi-Response Permutation Procedures (MRPP), and Indicator Species Analysis (ISA), were used to evaluate the effects of origin, management history, and conservation status on forest structure and species composition. Results indicated that multi-aged origin forests had significantly higher canopy tree diameters and deadwood volumes compared to even-aged origin stands, highlighting the benefits of varied-age management for structural diversity. Historically managed forests showed increased tree species richness, but lower deadwood volumes, suggesting a biodiversity–structure trade-off. Recent management, however, negatively impacted both deadwood volume and understory diversity, reflecting short-term forestry consequences. Protected areas exhibited higher deadwood volumes and bryophyte richness compared to commercial forests, indicating a small yet persistent effect of conservation strategies in sustaining forest complexity and biodiversity. Indicator species analysis identified specific vascular plants and bryophytes as markers of long-term management impacts. These findings highlight the ecological significance of integrating historical legacies and conservation priorities into modern management to support forest resilience and biodiversity.

Keywords: bryophytes; management history; Natura 2000 sites; vascular plants

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1. Introduction

The concept of forest ecological memory includes variety of modifications (called forest legacies) generated by both natural disturbances and anthropogenic management along with temporal aspects [1,2]. Historically there has been a significant shift in forest ecosystems from natural disturbances to more intense human-driven management approaches such as clear-cutting, selective harvesting, plantings, and understory maintenance [3]. Nowadays more forest land is protected [4] and clear cutting is transitioning into selective cutting or continuous cover forestry (CCF) [5]. CCF is not a new idea in forest management but there has been renewed interest in it for sustainability requirements [6,7]. It has also been found that sustainable forest management needs more region- and forest site type-specific targets [4,8].

Using historical data to quantify environmental impacts continues to be controversial [9], because of uncertain spatial accuracy, dates, and low image quality [10]. On the other hand, implications of historical management on forest structure and biodiversity are undeniable [11,12]. For example, ecosystem management has been shown to lead to retrogressive succession [13,14] and a simplified forest structure [15] but historical (ancient) semi-natural habitats, such as woodlands or grasslands, can support diverse communities and are key elements for biodiversity [16–18].

Already two decades ago, researchers recommended that anthropogenic disturbances in mature and old forest stands should receive more attention compared to the more extensively studied stand replacement cutting and natural disturbances [19–21]. Intensive structural and compositional changes also occur during the (re)establishment and growth of the stand [22], overshadowing the minor effects of internal stand modification and maintenance activities [23]. The manipulation of forest density, tree species composition, and other structural properties impact forest ecosystem complexity and various vegetation layers [24,25], and these effects are forest type-specific [26]. Forest management activities not only decrease habitat quality through the reduction in deadwood -a critical structural element for many species [27]—but also alter the species composition of field layer vegetation, bryophytes, lichens, and wood-inhabiting polypore fungi [26,28,29].

Estonia's forest ecosystems have undergone significant management transitions since the late 19th century. The study seeks to clarify the accumulating effect of forest management practices over the life-cycle time of an average stand in Estonia, tracing a cascade of management decisions from the period of the Russian Empire (beginning of the 20th century) to the current framework under the Republic of Estonia (Figure 1, Appendix A).

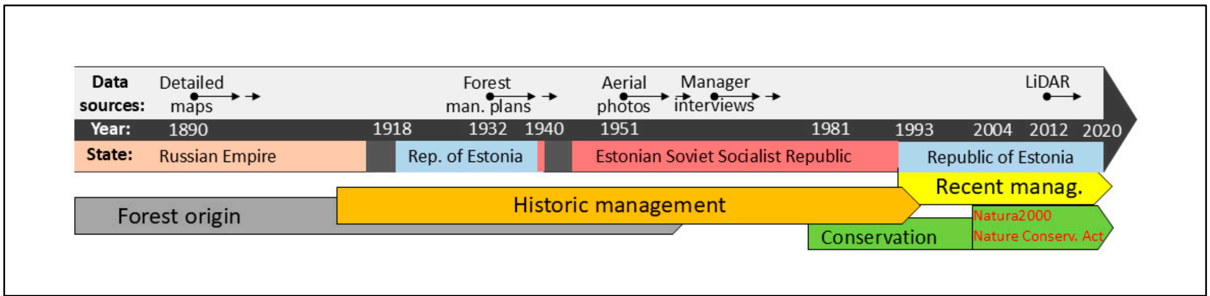

Figure 1. The timescale (state, year) and data (data sources) used for classifying (origin, management, conservation) study areas in Estonia.

Furthermore, Estonia's forest management has evolved from local collective farm and forest district management to a broader sector-based approach. For example, initially young forests (up to 20 years) undergo early tending and precommercial thinning [30], most systematically in planted and sowed conifer stands. This approach has started to evolve into more flexible cleaning and precommercial thinning of young stands, including those with naturally regenerated deciduous trees. Historical practices, such as seed tree harvest and selection thinning (developed by [31]), have been replaced by sanitation cutting across all ages and the more active use of clearcut and shelterwood silviculture in mature stands [32,33]. Recreational forest use has also gained prominence [34], with hiking and outdoor vacations complementing traditional activities such as berry/mushroom picking and herb gathering.

The Estonian Environmental Strategy 2030 indicates a complex turn towards sustainability, biodiversity conservation, and multifunctional forest use, marking a significant transformation need in Estonia's forest stewardship. The implications of this transition are necessary, not just for the sustainability of forest resources but also for Estonia's socio-economic landscape, setting a guideline for forest management in similar biogeographic contexts. Using a historical perspective, we examine the possibilities to shift from even-aged management to diverse, conservation-oriented strategies that align with modern ecological principles.

The first protected area in Estonia was established in 1910, the forest-oriented areas much later, and the establishment of new areas has continued through the 20th century [35]; however, in our study areas, the first conservation regulations began in 1981. Historically, forest protection zones were primarily managed at the district level, where forest land varied from 2000–4000 ha. Large nature preserves and landscape protection areas imposed various mild management restrictions. In addition to generic nature reserves and protection zones, specialized protected areas were established with the focus on water resources, natural maintenance, and key habitat protection. Since the 2000s, many areas have been reclassified as conservation zones or key habitat protection zones, bringing more specific regulations regarding cutting limitations and usage restrictions in sensitive areas such as road and water protection zones, recreational forests, and reserve coupes. The Nature Conservation Act (2004) categorizes protected areas into strict nature reserves, conservation zones, and limited management zones, specifying management restrictions in each.

In examining the long-term effects of forest management practices on the structure and biodiversity of Estonian hemiboreal forests, we categorize our study areas based on their stand origin, historical management, recent management, and conservation status (Figure 2).

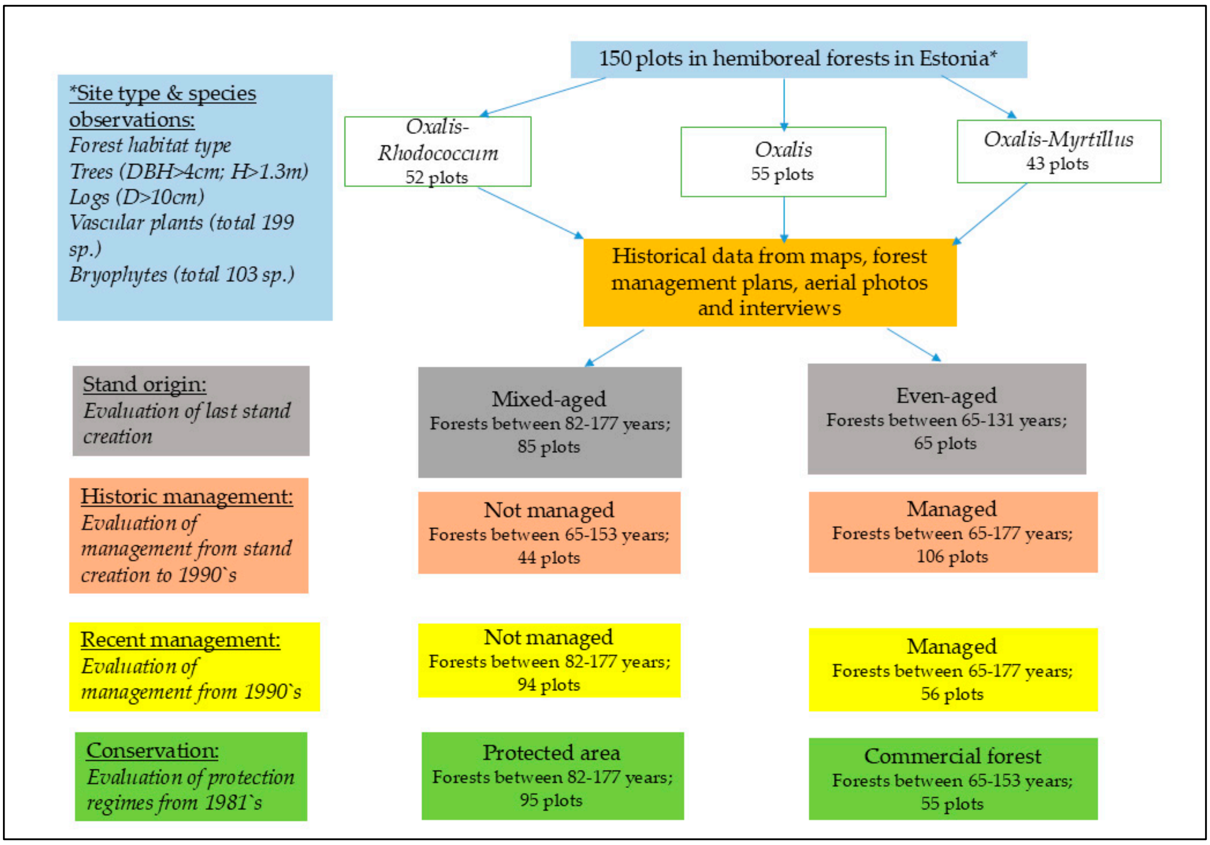

Figure 2. Study outline. Data (2015–2023) from 150 forest plots (blue) across various site types (white) and supplemented by historical data (orange) were used to classify plots into categories of stand origin (grey), historical management (brown), recent management (yellow), and conservation status (green).

Our study addresses the critical knowledge gap in understanding how long-term management practices, including historic and recent interventions, influence forest biodiversity and structure in Estonian hemiboreal forests. We hypothesize that multi-aged forests, as opposed to even-aged ones, will display higher biodiversity and structural complexity due to increased ecological continuity and varied habitat conditions. Additionally, we hypothesize that recent forest management will reduce biodiversity, while conservation practices will support higher deadwood volumes and species richness. We focused on the following research questions:

- How does multi-aged forest management influence biodiversity and forest structure compared to even-aged forests?
- What is the impact of historic management practices on current biodiversity and structural elements?
- How do recent management interventions affect deadwood volumes and species composition?
- How does conservation status contribute to biodiversity preservation in Estonian forests?

These objectives are essential for guiding future forest management strategies that balance production, conservation, and biodiversity goals.

2. Material and Methods

2.1. Study Region and Sample Plots

The study region is situated in eastern and southern Estonia (Figure 3). Estonia belongs to the hemiboreal vegetation zone [36]. The average annual precipitation is 550–750 mm per year^{-1}, with average temperatures ranging from 17 °C in July to −5 °C in February [37]. These forests are characterized by a mix of deciduous and coniferous trees, often including species like spruce, pine, birch, and aspen. Hemiboreal forests support a diverse range of flora and fauna, offering habitats that blend species typical of both boreal (northern) and temperate zones. This transitional nature of hemiboreal forests makes them particularly sensitive to environmental changes, offering a valuable indicator of ecological shifts due to climate and land-use changes. A recent study (2015–2023) selected 150 forest sites (plots with 15–30 m radius) in multiple forest areas. They belong to the Estonian Network of Forest Research Plots [38]. Study plots were located within each forest compartment, representing specific forest site type and different combinations of management histories (Figures 2 and 3). The recent study focused on three high-productivity forest site types: *Oxalis* (55 plots), *Oxalis-Myrtillus* (hereafter *Ox-Myrt*) (43 plots), and *Oxalis-Rhodococcum* (hereafter *Ox-Rhod*) (52 plots) [39,40]. Stands were limited to being at least 65 years old (average tree species age on plots varied from 65–177 years). The plots were then categorized by representation of differently managed forests and current conservation states (Figure 2).

In each plot, forest stands were characterized using the methodology of the Estonian Network of Forest Research Plots (ENFRP) [38]. Field works were carried out from June to September. Trees (including standing dead trees and broken dead trees at h > 1.3 m, i.e., snags) with a diameter at breast height (DBH) over 4 cm were recorded with the species, DBH, and height. In addition, all downed dead trees (logs) with a diameter over 10 cm at stump end were measured.

The sub-plot was positioned at the center of the stand plot. Pin-points were taken circularly extending from the center towards the perimeter at 1-m intervals. Ground-dwelling species of bryophytes and vascular plants were recorded. Their taxonomy followed the national reference textbooks [41,42]. Unidentified species were analyzed in the laboratory of the Estonian University of Life Sciences. Later, data on tree seedlings and bush species were excluded from the herb (field) layer data because they were also recorded in the forest understory data. In total, 199 vascular field layer plant species and 103 bryophyte species were identified.

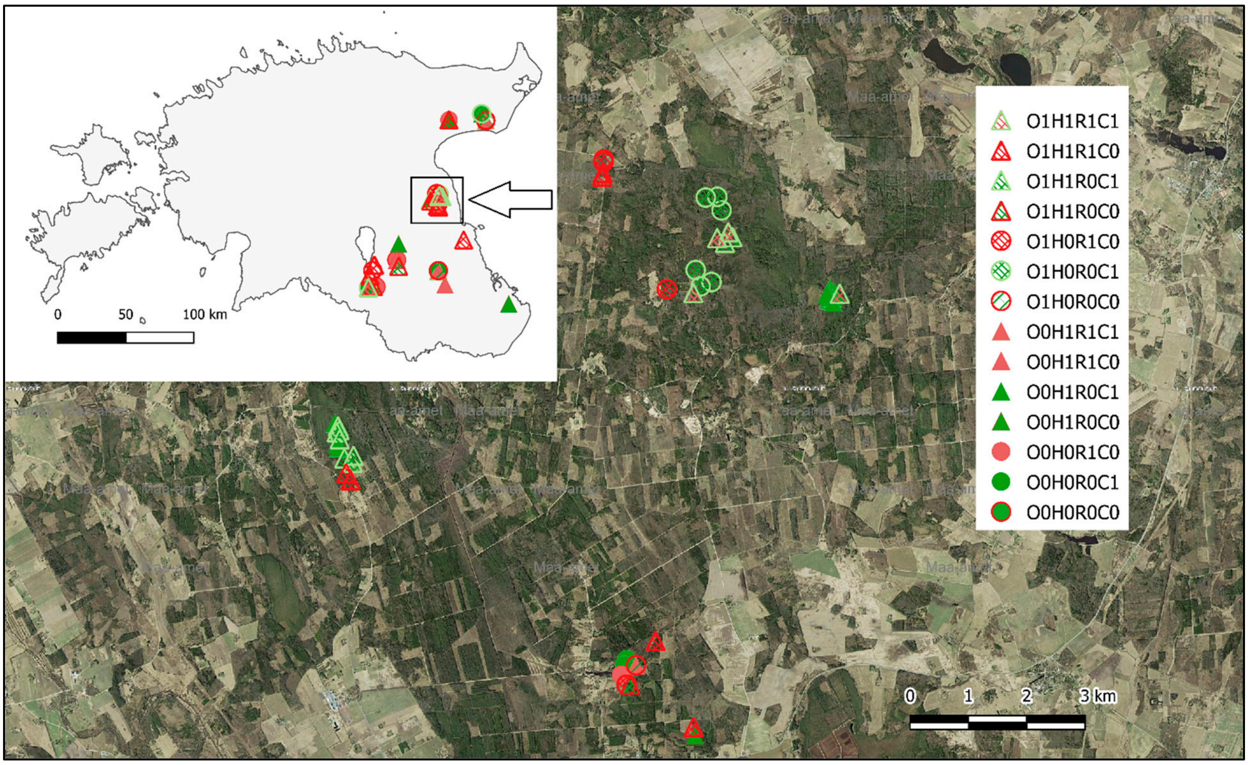

Figure 3. Location of the studied sample plots in Estonia. The map shows the geographic distribution of the 150 sample plots. Legend codes represent various management and conservation factors. O indicates stand historic origin, where 0 (solid fill) represents mixed-aged stands and 1 (pattern fill) represents even-aged stands. H represents historic management, with 0 (circle) for not managed and 1 (triangle) for managed. R stands for recent management, with 0 (green fill) for not managed and 1 (red fill) for managed. C represents conservation status, where 0 (red edge) indicates commercial forest and 1 (green edge) represents protected area.

2.2. Management History Assessment

Historical and recent forest management practices were assessed for the period from 1884 until recent survey (2015–2023 depending on plot). Management activities were categorized into binary variables to facilitate robust analysis (see Figure 2, Appendix A, Supplementary Materials). This approach reflects a simplification, acknowledging the continuum of management intensities; however, potential details would fall within the limits of main management steps, such as initiating the stand, maintenance of the stand for tree growth, and conservation. This historical assessment utilized a variety of sources (Appendix B), including historical maps, aerial photographs, and forest planning documents from the Estonian State Forest Center [43] and National Archives of Estonia [44]. Insights were improved by interviews with local forestry specialists (retired and working).

Management activities identified from State Forest maps and interviews ranged from early tending to selective cutting (Appendix A). For analysis, these activities were divided into the categories detectable and undetectable from aerial photographs. Activities such as large-scale cuttings were readily apparent on maps, contrasting with refined human interventions in forest stands that emerged from interview data. In our analysis, we focused on management actions detectable in aerial photographs, excluding the undetectable ones (Appendix A).

The timeline between historical to recent management was set to the 1990s to reflect sharp changes in the governmental system and forest management in Estonia. There was a significant shift from usage of clear-cuttings and wider use of forestry machines instead of manual labor. Alongside these shifts, forest conservation policy was revised following

Estonia's restoration of independence and joining the EU Natura 2000 legislation area, leading to an increase in strictly protected areas (Figure 1).

Management and conservation information was classified into categorical variables with four levels (Figure 2). Plots can be characterized either as commercial forests (55 plots) or protected sites (95 plots), including areas within the Natura 2000 network in Estonia. All the plots (96) in Natura 2000 forest sites represented the 9010* "Western Taiga" habitat type. Conservation information was categorized to reflect both commercial and protected areas. Protected sites are unmanaged according to the Nature Conservation Act (2004), which includes strict nature reserves and wilderness conservation areas. Commercial sites also include protected areas that permit some forms of forest management activities (limited management zones). We would like to note that the Natura 2000 habitat plots were surveyed in 2015, and by 2018, some of them (10 plots) were also managed as commercial forests. Currently, these Natura 2000 sites in Estonia are designated as Sites of Community Importance (SCI) but are expected to be reclassified as Special Areas of Conservation (SAC) [45]. The current management and protection statuses of the plots were used at the time (2015–2023) of recent survey. Classifications and main characteristics with found management histories for each plot can be found in Supplementary Materials.

2.3. Data Analysis

To explain the ecological requirements of vascular plants and bryophytes, we applied Ellenberg [46] indicator values. These values were estimated as community-weighted means for light and moisture requirements for both groups and for soil fertility value for vascular plants. Pin-point counts were used as abundances.

The structural characteristic of the forest stands and estimates of species richness were analyzed using a general linear mixed model (GLMM) [47]. The GLMM estimation using the Type I test was applied to test the cascading effect of factors, starting from the forest site type (as environmental envelope), stand origin, historic management, recent management, and ending with the present conservation status. Forestry region was included as a random factor to address spatial clustering of study sites and management styles within historic and present forest districts. Post hoc comparison analysis of mean estimates within factor were conducted using Tukey's multiple comparison test [48]. Analyses were preformed using the MIXED procedure implemented in SAS version 9.2 (SAS Institute Inc, Cary, North Carolina). To ensure comparability across variables, all continuous variables were standardized before analysis. The standardization allowed us to scale the predictors and the response variable appropriately, and while this typically constrains the effect sizes to a range between -1 and 1, certain variables exhibited strong associations, resulting in effect sizes and error bars exceeding this range. These larger effect sizes reflect the strong biological relationships between key environmental and management factors and the forest structure metrics under study. We assessed multicollinearity among the predictor variables using the variance inflation factor (VIF). All VIF values were below 5, indicating no significant multicollinearity. This ensures that the predictor variables are sufficiently independent, allowing for reliable coefficient estimation.

Non-metric multidimensional scaling (NMDS) was chosen as the ordination method to elucidate patterns in species composition. The species dataset included pinpoint counts representing the abundances of each species. Species compositional patterns in relation to stand origin, management, and conservation regimes were investigated using a multi-response permutation procedure (MRPP) [49]. In both analyses, the Bray–Curtis dissimilarity distance was applied on raw data, but the Euclidean distance was used on the species-plot semi-residual matrix, where the effect of site type and region was removed. Indicator species analysis (ISA) [50] was utilized to detect differences between same factors, with indicator values assessed for statistical significance through Monte Carlo permutation tests (1000 runs).

The NMDS, ISA, and MRPP analyses were executed using PC-ORD version 7.1 [51].

2.4. Manuscript Preparation

Generative AI technology was used in the preparation of this manuscript to assist with language editing, grammar correction, and structural refinement. Specifically, OpenAI's ChatGPT was employed to enhance the clarity and readability of the text, ensuring grammatical accuracy and consistency in terminology. No AI-generated content replaced the author's original scientific insights, data interpretations, or conclusions. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

3. Results

3.1. Environmental Envelope

The NMDS ordination (stress factor = 14.62, $p = 0.004$; Figure 4) resulted in a two-dimensional solution, capturing a significant portion (I axis 78%, II axis 10%) of the variation in field layer using raw logarithm data of vascular plants and bryophytes with species frequency > 3 on the plot ($n = 204$) and 25 environmental variables for species composition. The first axis is correlated with the plants' requirements for soil fertility and light availability and the second axis is correlated with the plants' requirements for soil moisture—these are conditions well related to the studied site types. It points out that the effect of forest site type on the analyzed species and structure is stronger and should be taken into account in the interpretation of the effects of the stand origin, management, or conservation (Figures 5 and 6; Appendix F).

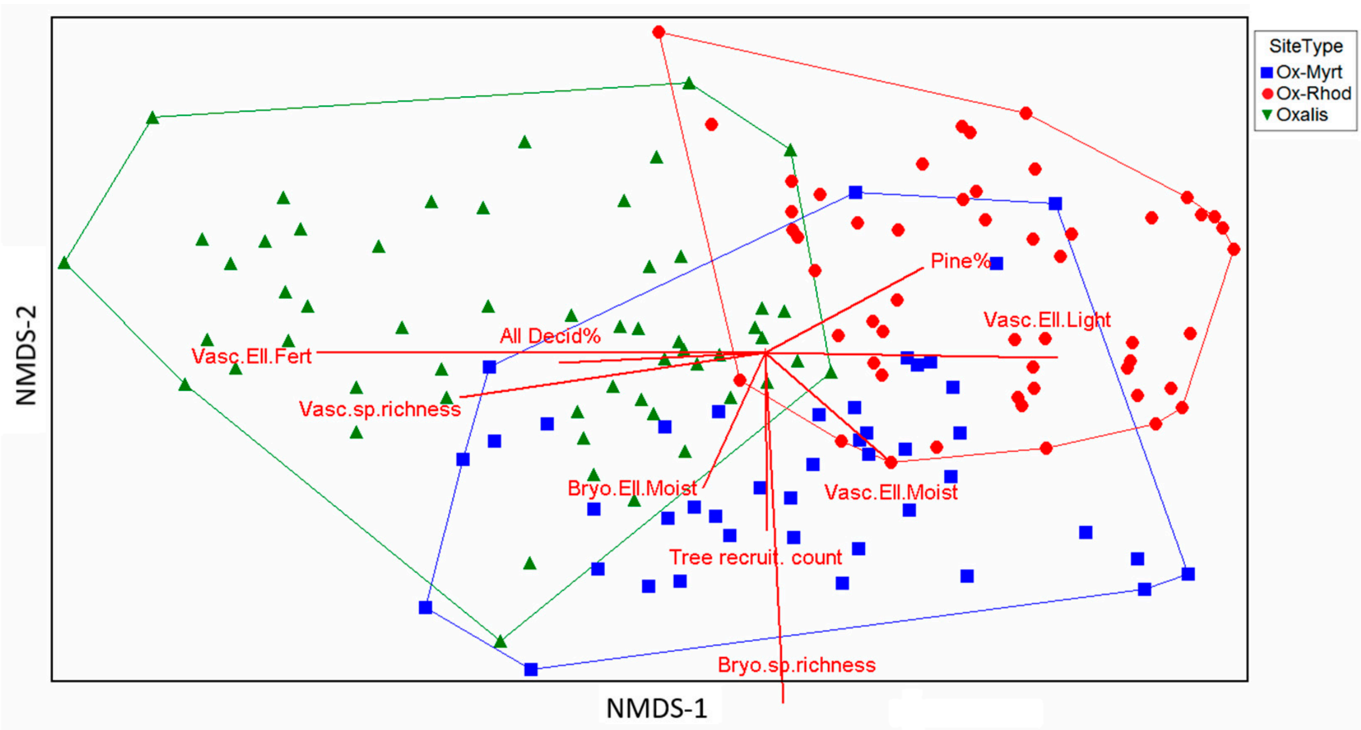

Figure 4. NDMS varimax ordination of 150 sample plots based on vascular plants and bryophytes. The first axis explains 78% of the variance ($p = 0.004$), while the second axis accounts for 10% of the variance ($p = 0.004$). The ordination was performed using raw logarithm data for species with a frequency >3 per plot (n = 204 species) and 25 environmental variables (see Appendix C for full list). Only environmental factors significantly related to the ordination axes ($p < 0.05$) are shown, with a cut-off of $R^2 = 0.2$ for vector inclusion. Plots are color-coded by site type: blue for *Ox-Myrt*, red for *Ox-Rhod*, and green for *Oxalis*. The pNDMS ordination without the effects of site type and region is available in Appendix F. The final stress value of the ordination is 14.62225, indicating the goodness of fit.

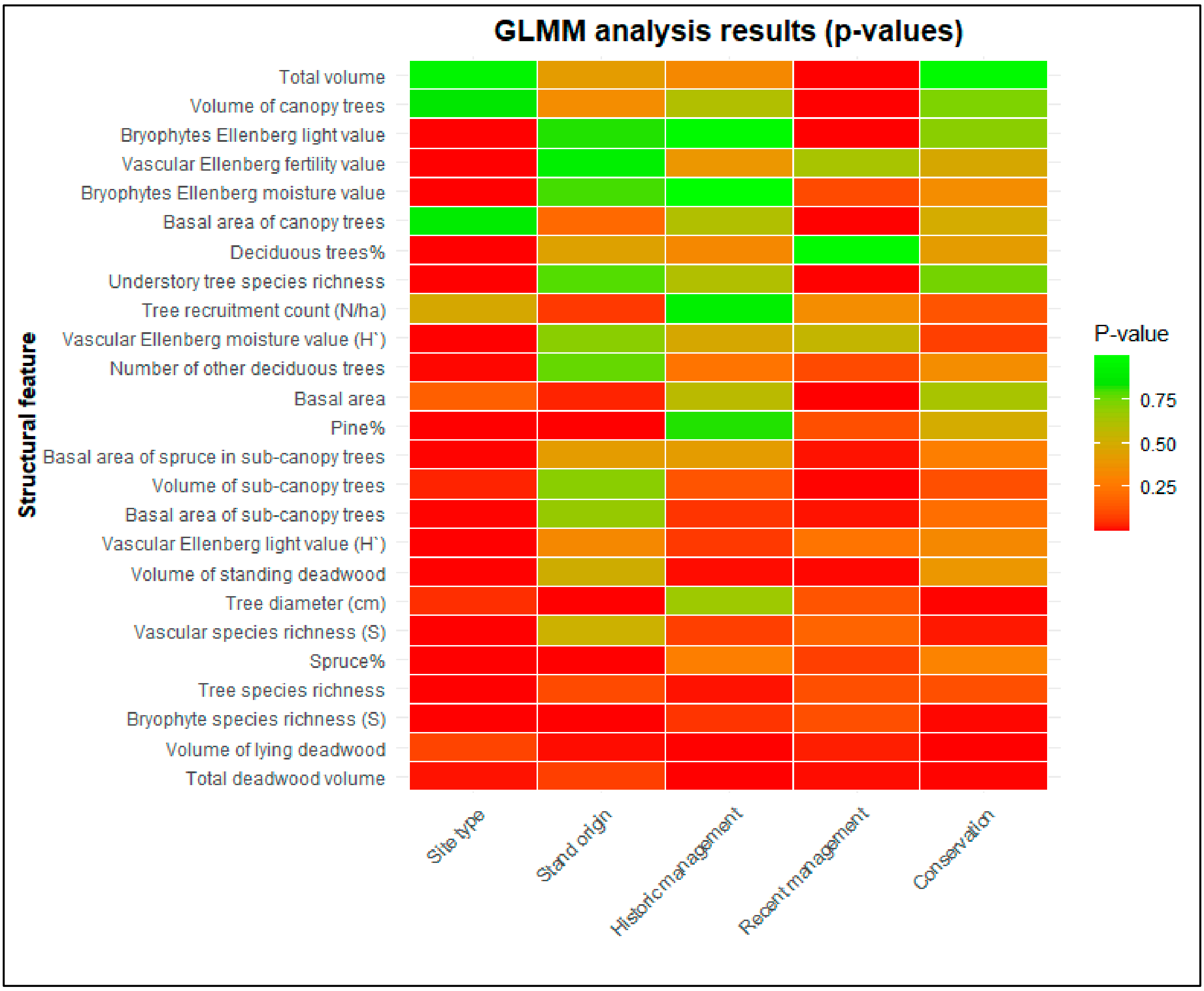

Figure 5. Heatmap showing GLMM analysis results (*p*-values) for each structural trait in different categories. The significant difference between sites was tested using the Type I model for structural traits. More detailed results in Appendix C.

3.2. Influence of Stand Origin on Forest Structure and Biodiversity

The results of General Linear Mixed Model (GLMM) analysis show that stand origin type predicts some forest structural and biodiversity features (Figures 5 and 6). Specifically, mixed-aged forests had differences in average diameter of canopy trees (GLMM, $p < 0.0001$), a 16% smaller proportion of pine and 12% greater proportion of spruce in the stand, and a 17.8 m^3/ha greater volume of lying deadwood (GLMM, $p = 0.011$) compared to even-aged stands (Appendix C, Figure 5). The basal area of canopy trees was 4.6 m^2 higher in mixed-aged stands. Also, bryophyte species richness was 4.9 species smaller in even-aged stands (GLMM, $p = 0.0003$).

The MRPP test (Figure 7) also showed differences in species composition between mixed-aged and even-aged forests' origin ($T = -7.1$, $p < 0.001$). ISA (Appendices D and E; Table 1), conducted for each site type separately, identified species such as *Dicranum majus*, *Rhizomnium punctatum*, and *Dicranum heteromalla* with higher frequency in multi-aged forests (ISA, $p < 0.05$). On the other hand, species such as *Melampyrum pratense* thrived in even-aged stands (ISA, $p < 0.001$).

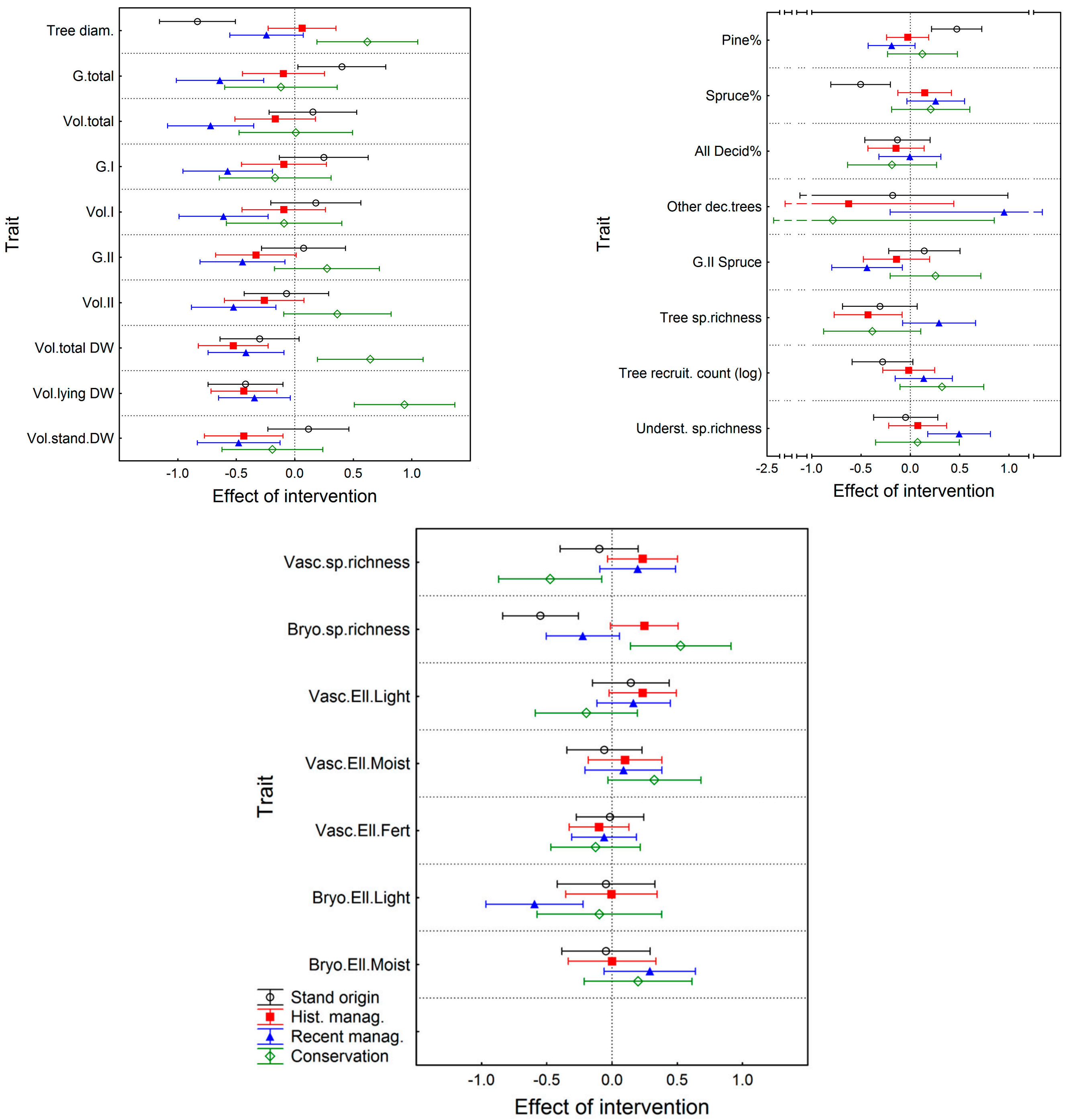

Figure 6. General Linear Mixed Model (GLMM) Type I tests to evaluate the effects of interventions (stand origin, historic and recent management, conservation) on the traits (structural features and biodiversity components) of forest stands). Each point indicates the mean effect size with its confidence interval, showing influence across traits. Variance inflation factor (VIF) values for all predictors were below 5, indicating no multicollinearity among the independent variables.

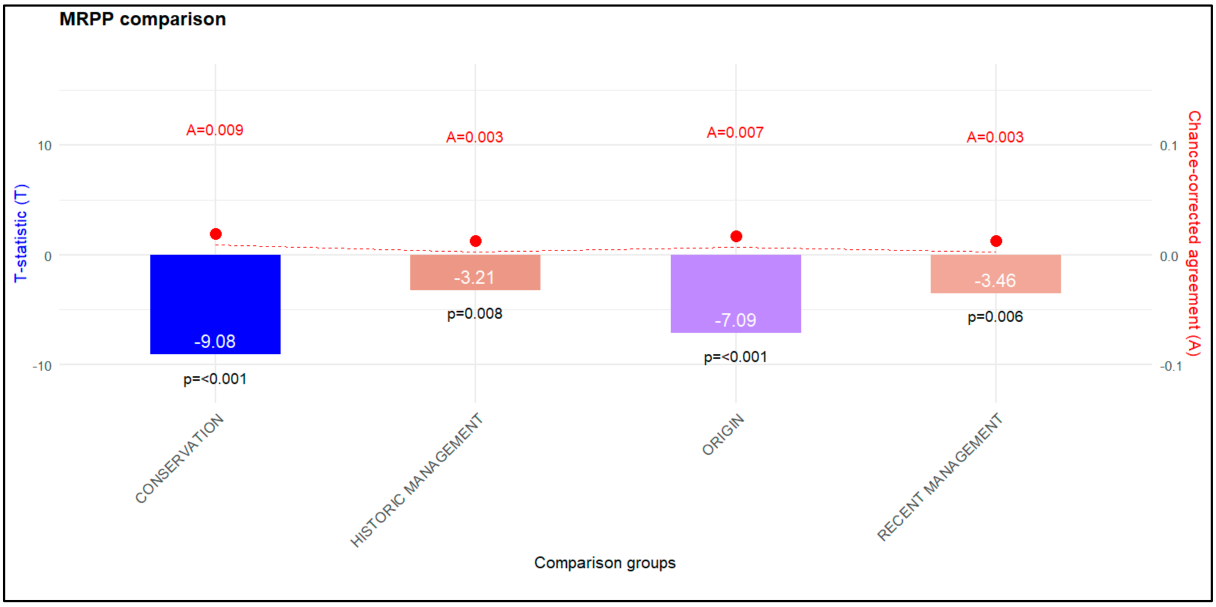

Figure 7. Multi-response permutation procedure (MRPP) results comparing species composition by different management regimes for stand origin, historic management, recent management, and conservation, with test statistic (T) and agreement (A) values.

Table 1. Summary of ISA (Indicator Species Analysis) results ($p < 0.05$) for different forest management regimes. The table summarizes species significantly associated with different management regimes for each habitat type. Habitats are indicated with superscripts: M for *Ox-Myrt*, O for *Oxalis*, and R for *Ox-Rhod*. For more detailed results of the ISA, please refer to Appendix D.

Factor: Historic Origin	
Level 0: Multi-Aged	**Level 1: Even-Aged**
Vascular plants: *Goodyera repens*^{R}, *Impatiens parviflora*^{O}, *Melampyrum nemorosum*^{MR}, *Moehringia trinervia*^{O}, *Orthilia secunda*^{O}, *Vaccinium vitis-idaea*^{O}, *Veronica chamaedrys*^{O}	Vascular plants: *Calluna vulgaris*^{R}, *Daphne mezereum*^{O}, *Dryopteris expansa*^{O}, *Galeobdolon luteum*^{O}, *Galium odoratum*^{O}, *Lathyrus vernus*^{O}, *Milium effusum*^{O}, *Pulmonaria obscura*^{O}, *Stellaria nemorum*^{O}, *Viola riviniana*^{O}
Bryophytes: *Brachythecium oedipodium*^{OR}, *Brachythecium salebrosum*^{O}, *Cirriphyllum piliferum*^{O}, *Dicranum heteromalla*^{M}, *Dicranum majus*^{MR}, *Dicranum montanum*^{OR}, *Lophocolea heterophylla*^{R}, *Nowellia curvifolia*^{OR}, *Plagiothecium curvifolium*^{R}, *Plagiothecium laetum*^{R}, *Ptilidium ciliare*, *Ptilium crista-castrensis*^{O}, *Ptilidium pulcherrimum*^{O,R}, *Rhizomnium punctatum*^{M}, *Sanionia uncinata*^{R}, *Tetraphis pellucida*^{O,R}	Bryophytes: -
Factor: Historic Management	
Level 0: Not Managed	**Level 1: Managed**
Vascular plants: *Molinia caerulea*^{M}, *Lathyrus vernus*^{O}	Vascular plants: *Angelica sylvestris*^{M}, *Carex vaginata*^{M}, *Convallaria majalis*^{M}, *Lycopodium annotinum*^{M}, *Melampyrum pratense*^{O}, *Moehringia trinervia*^{O}, *Mycelis muralis*^{O}, *Orthilia secunda*^{M}, *Rubus idaeus*^{O}
Bryophytes: *Hypnum cupressiforme*^{M}	Bryophytes: *Brachythecium oedipodium*^{M}, *Cirriphyllum piliferum*^{M}, *Plagiochila asplenioides*^{O}, *Pleurozium schreberi*^{O}

Table 1. *Cont.*

Factor: Recent Management	
Level 0: Not Managed	**Level 1: Managed**
Vascular plants: *Calluna vulgaris*^{R}, *Deschampsia flexuosa*^{M}, *Festuca ovina*^{R}, *Fragaria vesca*^{R}, *Goodyera repens*^{R}, *Orthilia secunda*^{O}	Vascular plants: *Aegopodium podagraria*^{M}, *Anemone nemorosa*^{M}, *Angelica sylvestris*^{M}, *Athyrium filix-femina*^{M}, *Calluna vulgaris*^{R}, *Carex digitata*^{M}, *Carex vaginata*^{M}, *Convallaria majalis*^{M}, *Crepis paludosa*^{M}, *Deschampsia cespitosa*^{M}, *Deschampsia flexuosa*^{R}, *Dryopteris filix-mas*^{O}, *Equisetum pratense*^{M}, *Equisetum sylvaticum*^{M}, *Fragaria vesca*^{M}, *Hepatica nobilis*^{M}, *Orthilia secunda*^{M}, *Rubus saxatilis*^{M}, *Solidago virgaurea*^{M}
Bryophytes: *Dicranum majus*^{M}, *Dicranum montanum*^{R}, *Lophocolea heterophylla*^{M}, *Nowellia curvifolia*^{R}, *Polytrichum commune*^{M}, *Ptilidium pulcherrimum*^{R}, *Sphagnum russowii*^{M}	Bryophytes: *Brachythecium oedipodium*^{R}, *Cirriphyllum piliferum*^{M}, *Dicranum majus*^{R}, *Dicranum montanum*^{R}, *Dicranum scoparium*^{R}, *Lophocolea heterophylla*^{R}, *Nowellia curvifolia*^{R}, *Plagiomnium affine*^{M}, *Plagiomnium ellipticum*^{MO}, *Plagiothecium curvifolium*^{R}, *Plagiothecium laetum*^{R}, *Ptilidium ciliare*^{R}, *Ptilidium pulcherrimum*^{R}, *Rhodobryum roseum*^{M}, *Sanionia uncinata*^{R}, *Tetraphis pellucida*^{R}
Factor: Conservation	
Level 1: Protected	**Level 0: Commercial**
Vascular plants: *Pteridium aquilinum*^{O}, *Orthilia secunda*^{O}	Vascular plants: *Dryopteris filix-mas*^{O}, *Impatiens parviflora*^{O}, *Stellaria nemorum*^{O}, *Urtica dioica*^{O}
Bryophytes: -	Bryophytes: *Eurhynchium angustirete*^{O}, *Plagiomnium ellipticum*^{O}

3.3. Impact of Historical Management

Forests with historical management showed higher tree species richness (GLMM, $p < 0.01$) and lower deadwood volumes (GLMM, $p < 0.05$) relative to historically unmanaged forests.

The ISA (Table 1) revealed significant associations between historically managed forests and certain species. Notable indicator species (Table 1, Appendix D) for historically managed forests was *Angelica sylvestris* (ISA, $p < 0.05$) and *Calamagrostis arundinacea* (ISA, $p < 0.01$). The bryophyte *Cirriphyllum piliferum* also showed high indicator values for historically managed forests (ISA, $p < 0.01$). Conversely, *Brachythecium oedipodium* and *Hypnum cupressiforme* (ISA, $p < 0.05$) implied their preference for more undisturbed conditions.

3.4. Effects of Recent Management

Understory tree species richness and basal area of spruce in sub-canopy trees showed a significant increase due to recent management activities (GLMM, $p < 0.01$). All variables connected to tree volume or basal area obviously showed lowering effects (Figure 6) under recent management (GLMM, $p < 0.01$). Also, all deadwood volumes were decreasing within plots where management after the 1990s was detected (GLMM, $p < 0.01$) (Appendix C).

ISA (Table 1, Appendix D) for recent management showed several species with strong relationships to recently managed forests. This suggests that management activities such as thinning, selective logging, and other interventions have an impact on analyzed species distributions. For instance, *Anemone nemorosa* showed a strong preference for recently managed areas, with a frequency of occurrence in these plots of 83% (ISA, $p < 0.001$). In the case of bryophytes, *Dicranum scoparium* was also found lot in recently managed forests, with a frequency of 94% (ISA, $p < 0.001$).

Within the management, the disparity was similar between historically (MRPP, $T = -3.2$, $p < 0.01$) and recently (MRPP, $T = -3.4$, $p < 0.01$) managed vs. unmanaged forests (Figure 7).

3.5. Protected Areas Outcomes

Protected areas exhibited higher average diameter of canopy trees compared to commercial forests, indicative of the positive impact of these practices on preserving larger trees (GLMM, $p < 0.01$). The volume of lying deadwood was significantly higher (GLMM,

$p < 0.0001$) in protected areas, averaging 59.1 m^3 ha^{-1} (Figure 5, Appendix C) compared to much lower average 22.3 m^3 ha^{-1} in commercial forests. Similarly (GLMM, $p < 0.01$), the total average volume of deadwood (77.6 m^3 ha^{-1}) in protected areas was 88% higher than in commercial forests (41.2 m^3 ha^{-1}). Bryophyte species richness was slightly higher in protected areas (GLMM, $p < 0.01$), contrary to the decrease in vascular plant species richness (GLMM, $p < 0.05$).

Indicator Species Analysis (ISA) also provided insights into how species that are indicative of conservation areas reflect the protective management regime's impact on maintaining or increasing biodiversity within these forest ecosystems. *Melampyrum pratense* and *Hylocomium splendens* were significantly associated with conservation areas, showing a high frequency of 100% (ISA, $p < 0.05$). These species are quite usual in Estonian forest ecosystems and despite finding protected species on some protected sites they did not occur in our ISA results. Notably, the species composition of commercial forests exhibited significant divergence from protected forests (MRPP, $T = -9.1$, $p < 0.001$).

4. Discussion

Our study of Estonian hemiboreal forests shows how long-term management practices influence forest structure and biodiversity, which is crucial for designing effective forest management policies. Our findings correlate with previous research on living and dead tree densities [52,53]. Contrary to study [27], our protected areas exhibited significant differences in deadwood volumes compared to commercial forest areas, indicating positive effects associated with protection. Our hypothesis that mixed stands would exhibit greater structural diversity, and that managed stands would have lower levels of forest structures, particularly deadwood, was confirmed. Contrary to our initial assumptions, ground vegetation species richness was not significantly affected by management. Bryophyte species richness was higher in protected areas, though the richness of herb layer species decreased.

Previous studies in boreal forests [26] have detected a nonlinear change in species composition response, indicative of a significant resilience in medium productivity site types. Also, Ref. [54] found a likely indirect pathway of edge effects through overstorey loss which led to shrub cover loss in the long term. This resilience may be attributed to the dominance of shrub and moss species like *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Hylocomium splendens*. Because of their broad ecological niches, these species are more tolerant of disturbances, thus significantly contributing to the overall resilience of the forest stands [55,56]. These findings offer insights into the ecosystems' natural resilience to anthropogenic impacts. Our results also support this viewpoint showing broad ecological niche species in different management regimes. For example, the presence of species like *Orthilia secunda* across various habitat conditions highlights their ecological adaptability, reflecting the intricate interplay between species and their environments. These dynamics are possibly influenced by the unique root systems of these plants, which engage in symbiotic relationships with mycorrhizal fungi, enhancing nutrient and water uptake. In turn, the fungi benefit from the carbohydrates produced by the plants through photosynthesis. The versatility of these species offers a valuable means to monitor diverse ecological states and assess the efficacy of various management approaches.

The transition in forestry processes has significantly impacted post-Soviet countries for decades [57–60]. Our research shows that forestry management actions such as sanitation, selection cutting, and thinning did not modify vascular and bryophyte species richness significantly. These findings do not suggest that recent management actions may become significant later, potentially being more substrate-based [61], or promoting vegetation growth [62]. Historical management actions conducted over 30 years ago have been shown to facilitate the restoration of vegetation composition in these stands, illustrating the resilience of historically and moderately managed forest stands [22]. This resilience is similar to our study observations in protected areas, where an increase in bryophyte richness and a decrease in vegetation richness indicate changes in substrate and light conditions.

Our findings about higher tree species richness in historical management sites suggest that these actions were more nature-based, creating more diverse species compositions. The scarcity of bryophytes and the presence of a larger scale of generalist species related to forest origin compared to historic management further endorse this idea [63]. Similarly to the findings of [64], we agree that in landscapes with long-term structures, forest species are less limited by dispersal and more by habitat characteristics. The species composition is influenced by the persistent presence of light, moisture, and fertility in the stand, determined by forest habitat type.

Our results show that in mature forests, the effect of forest age is more related to individual trees than to the entire stand. Individual trees are especially important for vascular plant species, which depend heavily on light conditions influenced by selected trees in past management actions. Selective cutting of canopy trees improves light availability, favoring regeneration and leading to a denser understory with an altered composition [65,66].

The significance of bryophyte richness from mixed-species origin and site protection has likely resulted from lower light access and different substrate base. This highlights the importance of considering the abundance, size, and decay stage distribution of coarse woody debris, which are key characteristics of natural forests [27,53] and support biodiversity [67,68]. The volume of deadwood increased under protection which suggests an enhancement of habitat complexity. Similar results, that forest protection increases deadwood volume and bryophyte species diversity, were also found by [69]. Like [70] we saw that management had the strongest negative effects on deadwood structures that occurred predominantly in the most productive forests like our study sites.

However, it is essential to acknowledge several limitations that merit consideration. The distinction between recent and historical management practices, influenced by the evolution of forestry machinery, introduces a variable that could influence the comparability of data across time. Although our study assumes ecological consistency across the research areas, aside from the effects of different habitat types and passive conservation measures, this simplification may not fully capture the complex interplay of ecological processes influencing forest dynamics. Moreover, our temporal overview, while comprehensive, may not capture the entirety of long-term ecological changes or the delayed effects of past management practices on the current composition and structure of forests. Future research should aim to incorporate more specific methodological approaches that can differentiate among various management practices over time and assess their individual impacts. Additionally, expanding the geographical and ecological scope of the study could enhance the applicability of future findings.

5. Conclusions

This study has systematically examined the long-term effects of different forest management practices on the biodiversity and structural complexity of Estonian hemiboreal forests. The results clearly demonstrate that multi-aged origin forests exhibit greater biodiversity and structural complexity compared to even-aged stands. This is driven by factors such as the higher average diameter of canopy trees, greater volumes of lying deadwood, and extended ecological continuity. These elements collectively support diverse plant communities, including a higher richness of bryophyte species and greater understory diversity, highlighting the critical role of habitat heterogeneity in promoting biodiversity.

Historically managed forests were found to have higher tree species richness but lower volumes of deadwood, suggesting a trade-off between species richness and structural complexity due to past disturbances. These findings show the importance of considering the long-lasting impacts of historical management when developing current forest management strategies.

Forests that have not undergone recent management interventions exhibited significantly higher levels of deadwood and understory diversity, confirming that recent management activities—particularly those implemented after the 1990s—tend to reduce tree volume and deadwood, impacting forest structure and biodiversity. In contrast, protected areas showed higher average diameters of canopy trees and greater volumes of both lying and standing deadwood. The bryophyte species richness was also higher in protected areas, although the richness of herb layer species decreased. These results bring out the importance of conservation-oriented management in maintaining habitat complexity and supporting ecological functions.

Our research offers several novel insights into the resilience and adaptability of forest ecosystems. For instance, species with broad ecological niches, such as *Orthilia secunda*, were prevalent across diverse management regimes, indicating their ability to thrive in various habitat conditions. These findings emphasize the need to manage multi-aged and protected forest stands with a focus on maintaining structural complexity and biodiversity.

In conclusion, successful forest management requires the integration of ecological insights and conservation priorities. By fostering landscapes that are productive, sustainable, and rich in biodiversity, forest management practices can better support ecosystem resilience and contribute to the long-term preservation of biodiversity in hemiboreal forests.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15112035/s1.

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Data Availability Statement: The datasets generated and analyzed during the current study are not publicly available due to institutional guidelines, but are available from the corresponding author on reasonable request.

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Conflicts of Interest: The authors declare that they have no conflicts of interest.

Appendix A

Historical and recent forest management and protection. Conservation regimes that allow forest management are written in italic. Forest management practices are also described [30,31,33] & Estonian Forest Act (2006). Protection regimes in Estonian Nature Conservation Act (2004).

Forest Management Activities (Detectable)			
Forest Age (Years)	**HISTORICAL**	**Forest Age (Years)**	**RECENT**
up to 10	Early tending (weed & release)	up to 10	Early tending (weed & release)
up to 10	Early tending (cleaning)	up to 20	Precommercial thin
from 11–20	Precommercial thin	from 20-mature stand	Commercial thin
from 21–40	Commercial thin	all ages	Sanitation cut
from 41–. . .	Selection thin	in mature stand	Selective cut
from 60–. . .	Sanitation cut	in mature stand	Clearcut
in mature stand	Selective cut (single tree)	in mature stand	Shelterwood cut
in mature stand	Clearcut	after clearcut	Seed tree harvest
after clearcut	Seed tree harvest		
Other Activities (Undetectable)			
Forest Age (Years)	**HISTORICAL**	**Forest Age (Years)**	**RECENT**
all ages	bud picking	all ages	hiking
all ages	seed collection	all ages	berry/mushroom picking
all ages	cone harvesting	all ages	herb picking
all ages	grazing	all ages	active vacation
all ages	firewood stock		
all ages	Household facilities (stick cutting; bath broom; besom etc.)		
all ages	berry/mushroom picking		
all ages	herb picking		
from 10–30	Trimming (prune)		
CONSERVATION			
HISTORICAL		**RECENT**	
reserve coupe		*water protection zone*	
road protection zone		protection area (natural)	
water protection zone		*protection area (maintenance)*	
esthetical/recreation forests		*buffer zone*	
landscape protection areas		reservation area	
nature conservation area/nature preserve		key habitat protection	

Appendix B

Used maps and aerial photos for the period of 1884–2022. Source: Estonian Land Board Web Map server since the 1880s (http://xgis.maaamet.ee/maps/XGis, accessed on 21 April 2024) and photo archives since the 1948s (https://fotoladu.maaamet.ee, accessed on 21 April 2024).

Map Types
Estonia/Rücker Livonia by Schmidt map (1884)
Verst map from the Russian Empire (1891–1912. scale 1:42,000)
Cadastral maps of the Estonian Republic (1930–1944. scale 1:42/50,000)
Topographic maps of Estonia (1923–1939. 1:50,000)

Map Types
Soviet topographic maps (1942 reference system) in scales 1:10,000. 1:25,000. 1:50,000. 1:100,000. 1:200,000. 1: 300,000. 1:500,000. 1:1 000,000; all printed between 1946 and 1989. 1:100,000 printed between 1898 and 1989
Soviet topographic maps (1963 reference system) in scales 1:10,000 and 1:25,000 (printed between 1966 and 1987)
Estonian Base Map 1:50,000 (1994–1998)
Map of Estonia 1:50,000 (ordered by Estonian Defense Forces 1997–2003)
Estonian Basic Map 1:10,000 yearly versions (1996–2007 and since 2009 to nowadays)
Estonian Basic Map 1:20,000 (paper version. printed between 1994 and 2022)
Cadastral maps (schematic map 1930–1944. 1978–1989)
Soil map. Land Board 2001
Aerial photos and models
Arial photo archives (since the 1940s–1992) Photo plans (1942–1991) Land Board Orthophotos (2002–2022) Historical satellite images (since 1965–1993) Land Board Elevation Data 2017–2020 (height points. contours. depth points. depth contours) Canopy Height Model—CHM Digital Surface Model—DSM; visible in zoon scales 0 to 24,000) Hillshading (2008–2012. 2012–2015) Digital terrain model (2011–2014)

Appendix C

Plots (n = 150) variables and abbreviations.

Abbreviation	Variables	Unit	Average	Standard Dev.	Lower Quartile	Median	Higher Quartile
Tree Diam	diameter (DBH) of canopy trees	cm	36.3	5.2	32.6	35.4	39.1
G.total	Basal area of trees over 5 m of height	$m^2\ ha^{-1}$	36.9	8.5	31.7	37.2	42.1
Vol.total	Volume of trees over 5 m of height	$m^3\ ha^{-1}$	478.8	127.7	386.2	472.8	557.7
G.I	Basal area of canopy trees	$m^2\ ha^{-1}$	30.9	8.1	26.4	30.8	35.9
Vol.I	Volume of canopy trees	$m^3\ ha^{-1}$	423.2	123.0	335.4	420.3	502.9
G.II	Basal area of sub-canopy trees (trees reaching height of 25–75% of canopy layer)	$m^2\ ha^{-1}$	6.0	3.1	3.8	5.3	8.0
Vol.II	Volume of sub-canopy trees (trees reaching height of 25–75% of canopy layer)	$m^3\ ha^{-1}$	55.6	30.5	31.9	49.0	74.0
All Decid%	Percentage of deciduous trees by volume	%	18.8	24.4	1.4	8.5	25.6
Spruce%	Percentage of Norway spruce by volume	%	31.9	24.3	13.0	25.7	44.2
Pine%	Percentage of Scots pine by volume	%	49.2	34.4	7.6	58.0	78.3
Other dec.trees	Number of non-commercial deciduous trees		0.3	0.5	0.0	0.0	1.0

Abbreviation	Variables	Unit	Average	Standard Dev.	Lower Quartile	Median	Higher Quartile
Tree sp.richness	Number of tree species		4.3	1.1	4.0	4.0	5.0
G.II spruce	Basal area of spruce in sub-canopy trees (trees reaching height of 25–75% of canopy layer)	$m^2\ ha^{-1}$	5.2	3.0	4.5	7.3	2.9
Understory sp.rich.	Number of tree species in forest understory (height under 4 m)		2.2	1.0	2.0	3.0	1.8
Tree recruit.count	Number of trees in forest understory (height under 4 m)	$N\ ha^{-1}$	373.3	85.5	268.8	507.0	610.7
Vol.lying DW	Volume of lying dead wood (over 10 cm at stump end)	$m^3\ ha^{-1}$	45.6	42.2	13.1	37.4	64.9
Vol.stand.DW	Volume of standing dead wood (over 4 cm DBH)	$m^3\ ha^{-1}$	18.6	18.4	5.7	13.9	26.6
Vol.total DW	Volume of total dead wood (lying & standing)	$m^3\ ha^{-1}$	64.2	50.6	25.7	58.7	85.5
Vasc.sp.richness	Vascular species richness on plot	S	22.0	10.4	14.0	21.0	29.0
Bryo.sp.richness	Bryophytes species richness on plot	S	14.1	8.9	6.0	14.0	22.0
Vasc.Ell.Light	Herb layer weighted average Ellenberg light value		4.4	0.8	3.9	4.7	5.1
Vasc.Ell.Moist	Herb layer weighted average Ellenberg moisture value		5.4	0.3	5.2	5.3	5.6
Vasc.Ell.Fert	Herb layer weighted average Ellenberg nitrogen value		3.9	0.9	3.0	3.9	4.7
Bryo.Ell.Light	Bryophytes weighted average Ellenberg light value		5.5	0.9	5.4	5.7	5.9
Bryo.Ell.Moist	Bryophytes weighted average Ellenberg moisture value		4.4	0.8	4.1	4.3	4.7

Detailed GLMM analysis results (p-values) for each structural trait. The significant difference between sites was tested using Type I model for structural traits. Bold numbers indicate significant differences $p < 0.01$ in the analysis results.

Structural Feature	Unit	Site Type	Stand Origin	Historic Management	Recent Management	Conservation
Tree diameter	cm	0.0533	**<0.0001**	0.6684	0.1305	**0.0053**
Basal area	$m^2\ ha^{-1}$	0.166	**0.0372**	0.5876	**0.001**	0.6321
Total volume	$m^3\ ha^{-1}$	0.9402	0.4139	0.3392	**0.0002**	0.9685
Basal area of canopy trees	$m^2\ ha^{-1}$	0.8706	0.1991	0.6159	**0.0038**	0.4927
Volume of canopy trees	$m^3\ ha^{-1}$	0.8556	0.3578	0.6043	**0.002**	0.718
Basal area of sub-canopy trees	$m^2\ ha^{-1}$	**0.0058**	0.678	0.0594	**0.0166**	0.2311
Volume of sub-canopy trees	$m^3\ ha^{-1}$	**0.0349**	0.6996	0.1316	**0.005**	0.1228
Pine%	%	**<0.0001**	**0.0003**	0.8063	0.1188	0.4911
Spruce%	%	**<0.0001**	**0.0013**	0.2883	0.0835	0.303

Structural Feature	Unit	Site Type	Stand Origin	Historic Management	Recent Management	Conservation
Deciduous trees%	%	**0.0009**	0.4384	0.3203	0.9815	0.4192
Number of other deciduous trees		**0.009**	0.7624	0.2483	0.1059	0.3449
Tree species richness		**0.001**	0.1102	**0.0153**	0.1215	0.1271
Basal area of spruce in sub-canopy trees	$m^2\ ha^{-1}$	**0.0053**	0.4347	0.4131	**0.017**	0.2754
Understory tree species richness		**<0.0001**	0.7769	0.614	**0.0025**	0.7357
Tree recruitment count	$N\ ha^{-1}$	0.4842	0.0736	0.9082	0.3514	0.1374
Volume of lying deadwood	$m^3\ ha^{-1}$	0.0996	**0.0106**	**0.0028**	**0.0287**	**<0.0001**
Volume of standing deadwood	$m^3\ ha^{-1}$	**0.0026**	0.5082	**0.0116**	**0.0087**	0.3901
Total deadwood volume	$m^3\ ha^{-1}$	0.0146	0.0817	**0.0007**	0.0123	**0.0056**
Vascular species richness	S	**<0.0001**	0.5243	0.0854	0.1824	**0.0204**
Bryophyte species richness	S	**<0.0001**	**0.0003**	0.0594	0.1193	**0.0082**
Vascular Ellenberg light value	H′	**<0.0001**	0.3275	0.0738	0.2462	0.3264
Vascular Ellenberg moisture value	H′	**<0.0001**	0.6932	0.483	0.5528	0.0818
Vascular Ellenberg fertility value		**<0.0001**	0.9121	0.3953	0.6361	0.4722
Bryophytes Ellenberg light value		**0.0026**	0.8148	0.9815	**0.0021**	0.6929
Bryophytes Ellenberg moisture value		**0.0015**	0.7908	0.9934	0.105	0.3478

Appendix D

Detailed ISA analyses of classifying categories (stand origin—ORIGIN, historic management—HISTORIC, recent management—RECENT, Conservation—CONSERV.; Figure 2) and habitat (*Ox-Myrtc*, *Oxalis*, *Ox-Rhod*) species with frequency (FR) and indicator value (IV) to specific group (0/1) with significance (*p**). Species and group abbreviations list with corresponding Latin names is given in Appendix E.

Feature	Habitat	Species	FR0	FR1	IV0	IV1	*p**	Group
ORIGIN	*Ox-Myrt*	*Dicr maju*	59	21	46	5	0.0382	Bryo
ORIGIN	*Ox-Myrt*	*Rhiz punc*	31	0	31	0	0.0374	Bryo
ORIGIN	*Ox-Myrt*	*Dicr hete*	34	0	34	0	0.018	Bryo
ORIGIN	*Ox-Myrt*	*Mela nemo*	38	0	38	0	0.0152	Vasc
ORIGIN	*Ox-Myrt*	*Mela prat*	38	100	8	79	0.0002	Vasc
ORIGIN	*Ox-Myrt*	*Dicr scop*	100	86	58	36	0.0164	Bryo
ORIGIN	*Ox-Myrt*	*Plag aspl*	79	64	55	19	0.048	Bryo
ORIGIN	*Ox-Myrt*	*Ptil pulc*	83	43	53	16	0.0352	Bryo
ORIGIN	*Oxalis*	*Gale lute*	31	65	10	44	0.0112	Vasc
ORIGIN	*Oxalis*	*Mili effu*	28	58	8	42	0.0142	Vasc
ORIGIN	*Oxalis*	*Daph meze*	17	54	4	42	0.0032	Vasc
ORIGIN	*Oxalis*	*Dryo expa*	21	54	5	41	0.0074	Vasc
ORIGIN	*Oxalis*	*Lath vern*	14	50	2	44	0.0012	Vasc
ORIGIN	*Oxalis*	*Viol rivi*	21	50	5	38	0.0198	Vasc
ORIGIN	*Oxalis*	*Gali odor*	7	35	0	32	0.0052	Vasc

Feature	Habitat	Species	FR0	FR1	IV0	IV1	*p**	Group
ORIGIN	*Oxalis*	*Pulm obsc*	14	35	2	29	0.0214	Vasc
ORIGIN	*Oxalis*	*Stel nemo*	14	35	2	29	0.0462	Vasc
ORIGIN	*Oxalis*	*Dicr mont*	66	31	45	10	0.015	Bryo
ORIGIN	*Oxalis*	*Ptil cri-c*	48	27	36	7	0.0348	Bryo
ORIGIN	*Oxalis*	*Vacc viti*	62	27	48	6	0.003	Vasc
ORIGIN	*Oxalis*	*Ptil pulc*	59	23	41	7	0.0114	Bryo
ORIGIN	*Oxalis*	*Moeh trin*	45	19	31	6	0.049	Vasc
ORIGIN	*Oxalis*	*Cirr pili*	52	19	43	3	0.0036	Bryo
ORIGIN	*Oxalis*	*Impa parv*	52	15	46	2	0.0008	Vasc
ORIGIN	*Oxalis*	*Brac oedi*	55	15	38	5	0.0148	Bryo
ORIGIN	*Oxalis*	*Vero cham*	41	12	32	3	0.0234	Vasc
ORIGIN	*Oxalis*	*Brac sale*	31	8	25	1	0.0358	Bryo
ORIGIN	*Oxalis*	*Orth secu*	34	8	31	1	0.008	Vasc
ORIGIN	*Oxalis*	*Tetr pell*	38	8	32	1	0.011	Bryo
ORIGIN	*Oxalis*	*Nowe curv*	41	4	39	0	0.0008	Bryo
ORIGIN	*Oxalis*	*Oxal acet*	100	100	47	53	0.0048	Vasc
ORIGIN	*Oxalis*	*Hylo sple*	90	73	54	29	0.0346	Bryo
ORIGIN	*Ox-Rhod*	*Call vulg*	19	44	5	32	0.0412	Vasc
ORIGIN	*Ox-Rhod*	*Good repe*	63	12	53	2	0.0002	Vasc
ORIGIN	*Ox-Rhod*	*Ptil pulc*	78	8	71	1	0.0002	Bryo
ORIGIN	*Ox-Rhod*	*Mela nemo*	37	4	28	1	0.03	Vasc
ORIGIN	*Ox-Rhod*	*Brac oedi*	41	4	39	0	0.0016	Bryo
ORIGIN	*Ox-Rhod*	*Ptil cili*	44	4	41	0	0.0016	Bryo
ORIGIN	*Ox-Rhod*	*Tetr pell*	44	4	41	0	0.0012	Bryo
ORIGIN	*Ox-Rhod*	*Dicr maju*	48	4	45	0	0.0002	Bryo
ORIGIN	*Ox-Rhod*	*Loph hete*	52	4	49	0	0.0002	Vasc
ORIGIN	*Ox-Rhod*	*Plat laet*	56	4	52	0	0.0008	Bryo
ORIGIN	*Ox-Rhod*	*Plat curv*	41	0	41	0	0.0006	Bryo
ORIGIN	*Ox-Rhod*	*Sani unci*	44	0	44	0	0.0004	Bryo
ORIGIN	*Ox-Rhod*	*Dicr mont*	63	0	63	0	0.0002	Bryo
ORIGIN	*Ox-Rhod*	*Nowe curv*	74	0	74	0	0.0002	Bryo
ORIGIN	*Ox-Rhod*	*Vacc myrt*	100	100	42	58	0.0002	Vasc
ORIGIN	*Ox-Rhod*	*Pleu schr*	100	100	45	55	0.0174	Bryo
ORIGIN	*Ox-Rhod*	*Hylo sple*	100	100	46	54	0.0038	Bryo
ORIGIN	*Ox-Rhod*	*Vacc viti*	89	96	35	59	0.0122	Vasc
ORIGIN	*Ox-Rhod*	*Mela prat*	74	80	23	55	0.0236	Vasc
ORIGIN	*Ox-Rhod*	*Conv maja*	44	76	10	58	0.0012	Vasc
ORIGIN	*Ox-Rhod*	*Dicr poly*	100	60	56	26	0.015	Bryo
ORIGIN	*Ox-Rhod*	*Dicr scop*	85	44	54	16	0.01	Bryo
ORIGIN	*Ox-Rhod*	*Ptil cri-c*	93	44	60	15	0.0006	Bryo
HISTORIC	*Ox-Myrt*	*Cirr pili*	20	73	2	66	0.0022	Bryo

Feature	Habitat	Species	FR0	FR1	IV0	IV1	*p**	Group
HISTORIC	*Ox-Myrt*	*Brac oedi*	30	70	7	53	0.047	Bryo
HISTORIC	*Ox-Myrt*	*Lyco anno*	0	64	0	64	0.0022	Vasc
HISTORIC	*Ox-Myrt*	*Conv maja*	0	52	0	52	0.0124	Vasc
HISTORIC	*Ox-Myrt*	*Orth secu*	10	48	1	44	0.0416	Vasc
HISTORIC	*Ox-Myrt*	*Care vagi*	0	45	0	45	0.02	Vasc
HISTORIC	*Ox-Myrt*	*Ange sylv*	0	39	0	39	0.0432	Vasc
HISTORIC	*Ox-Myrt*	*Hypn cupr*	50	12	40	2	0.0224	Bryo
HISTORIC	*Ox-Myrt*	*Moli caer*	60	9	54	1	0.0004	Vasc
HISTORIC	*Ox-Myrt*	*Cala arun*	90	100	36	60	0.0016	Vasc
HISTORIC	*Ox-Myrt*	*Rhyt triq*	60	79	16	57	0.0384	Bryo
HISTORIC	*Oxalis*	*Pleu schr*	27	83	7	62	0.0018	Bryo
HISTORIC	*Oxalis*	*Rubu idae*	27	73	7	55	0.01	Vasc
HISTORIC	*Oxalis*	*Myce mura*	13	58	1	52	0.0032	Vasc
HISTORIC	*Oxalis*	*Plag aspl*	20	58	4	45	0.032	Bryo
HISTORIC	*Oxalis*	*Moeh trin*	7	43	1	35	0.0456	Vasc
HISTORIC	*Oxalis*	*Mela prat*	0	30	0	30	0.039	Vasc
HISTORIC	*Oxalis*	*Lath vern*	47	25	36	6	0.0328	Vasc
HISTORIC	*Oxalis*	*Cala arun*	100	100	44	56	0.0136	Vasc
HISTORIC	*Oxalis*	*Hylo sple*	60	90	20	60	0.0074	Bryo
HISTORIC	*Oxalis*	*Vacc myrt*	67	88	24	56	0.0442	Vasc
HISTORIC	*Oxalis*	*Frag vesc*	47	75	15	51	0.0442	Vasc
HISTORIC	*Oxalis*	*Rhyt triq*	33	65	9	48	0.0448	Bryo
HISTORIC	*Oxalis*	*Anem nemo*	93	65	61	22	0.0042	Vasc
HISTORIC	*Ox-Rhod*	*Luzu pilo*	68	97	28	57	0.027	Vasc
RECENT	*Ox-Myrt*	*Anem nemo*	32	83	5	69	0.0002	Vasc
RECENT	*Ox-Myrt*	*Soli virg*	28	72	8	70	0.0002	Vasc
RECENT	*Ox-Myrt*	*Crep palu*	12	67	0	50	0.0006	Vasc
RECENT	*Ox-Myrt*	*Athy fili*	20	67	4	55	0.001	Vasc
RECENT	*Ox-Myrt*	*Plag affi*	24	61	2	53	0.0008	Bryo
RECENT	*Ox-Myrt*	*Dicr maju*	20	61	61	2	0.0006	Bryo
RECENT	*Ox-Myrt*	*Loph hete*	16	61	46	7	0.0238	Vasc
RECENT	*Ox-Myrt*	*Ange sylv*	12	56	2	44	0.003	Vasc
RECENT	*Ox-Myrt*	*Desc flex*	28	56	58	17	0.0122	Vasc
RECENT	*Ox-Myrt*	*Equi prat*	0	50	1	34	0.008	Vasc
RECENT	*Ox-Myrt*	*Rhod rose*	20	50	11	61	0.0032	Bryo
RECENT	*Ox-Myrt*	*Desc cesp*	0	44	3	31	0.0388	Bryo
RECENT	*Ox-Myrt*	*Cirr pili*	0	44	10	65	0.0006	Bryo
RECENT	*Ox-Myrt*	*Aego poda*	8	39	2	29	0.0364	Vasc
RECENT	*Ox-Myrt*	*Orth secu*	8	39	5	47	0.006	Vasc
RECENT	*Ox-Myrt*	*Frag vesc*	12	39	8	52	0.0046	Vasc
RECENT	*Ox-Myrt*	*Equi sylv*	0	39	9	62	0.0014	Vasc

Feature	Habitat	Species	FR0	FR1	IV0	IV1	*p**	Group
RECENT	*Ox-Myrt*	*Rubu saxa*	0	39	12	62	0.0014	Vasc
RECENT	*Ox-Myrt*	*Conv maja*	0	33	6	43	0.014	Vasc
RECENT	*Ox-Myrt*	*Plag elli*	0	28	1	45	0.0018	Bryo
RECENT	*Ox-Myrt*	*Hepa nobi*	0	28	5	44	0.0088	Vasc
RECENT	*Ox-Myrt*	*Spha russ*	0	22	37	2	0.0244	Bryo
RECENT	*Ox-Myrt*	*Poly comm*	0	22	41	2	0.0104	Bryo
RECENT	*Ox-Myrt*	*Care digi*	0	22	19	53	0.0292	Vasc
RECENT	*Ox-Myrt*	*Care vagi*	44	11	1	58	0.0004	Vasc
RECENT	*Ox-Myrt*	*Cala arun*	96	100	41	58	0.0022	Vasc
RECENT	*Ox-Myrt*	*Spha girg*	36	89	50	6	0.0104	Bryo
RECENT	*Ox-Myrt*	*Tetr pell*	44	83	44	6	0.0262	Bryo
RECENT	*Ox-Myrt*	*Rhyt triq*	44	83	23	56	0.023	Bryo
RECENT	*Ox-Myrt*	*Care glob*	60	78	39	1	0.016	Vasc
RECENT	*Ox-Myrt*	*Rubu idae*	44	78	5	37	0.0334	Vasc
RECENT	*Ox-Myrt*	*Gymn dryo*	80	61	5	45	0.0066	Vasc
RECENT	*Oxalis*	*Dryo fili*	32	52	9	38	0.0474	Bryo
RECENT	*Oxalis*	*Plag elli*	14	48	4	36	0.0156	Bryo
RECENT	*Oxalis*	*Orth secu*	32	11	25	2	0.0472	Vasc
RECENT	*Oxalis*	*Luzu pilo*	89	96	38	55	0.0358	Vasc
RECENT	*Oxalis*	*Dryo cart*	86	93	32	58	0.0096	Bryo
RECENT	*Oxalis*	*Rubu saxa*	100	85	60	34	0.001	Vasc
RECENT	*Oxalis*	*Plag affi*	36	67	13	43	0.0372	Bryo
RECENT	*Ox-Rhod*	*Dicr scop*	20	94	4	74	0.0002	Bryo
RECENT	*Ox-Rhod*	*Ptil pulc*	0	72	0	72	0.0002	Bryo
RECENT	*Ox-Rhod*	*Call vulg*	22	64	4	51	0.005	Vasc
RECENT	*Ox-Rhod*	*Nowe curv*	0	63	0	63	0.0002	Bryo
RECENT	*Ox-Rhod*	*Dicr mont*	0	53	0	53	0.0002	Bryo
RECENT	*Ox-Rhod*	*Plat laet*	0	50	0	50	0.0002	Bryo
RECENT	*Ox-Rhod*	*Loph hete*	0	47	0	47	0.0006	Vasc
RECENT	*Ox-Rhod*	*Desc flex*	0	44	0	44	0.0016	Vasc
RECENT	*Ox-Rhod*	*Dicr maju*	0	44	0	44	0.0014	Bryo
RECENT	*Ox-Rhod*	*Ptil cili*	0	41	0	41	0.0018	Bryo
RECENT	*Ox-Rhod*	*Tetr pell*	0	41	0	41	0.0022	Bryo
RECENT	*Ox-Rhod*	*Brac oedi*	0	38	0	38	0.0036	Bryo
RECENT	*Ox-Rhod*	*Sani unci*	0	38	0	38	0.0046	Bryo
RECENT	*Ox-Rhod*	*Plat curv*	0	34	0	34	0.0028	Bryo
RECENT	*Ox-Rhod*	*Call vulg*	45	22	39	3	0.0106	Vasc
RECENT	*Ox-Rhod*	*Frag vesc*	50	19	45	2	0.002	Vasc
RECENT	*Ox-Rhod*	*Fest ovin*	70	13	66	1	0.0002	Vasc
RECENT	*Ox-Rhod*	*Good repe*	46	9	42	1	0.039	Vasc
RECENT	*Ox-Rhod*	*Ptil pulc*	54	9	47	1	0.0374	Bryo

Feature	Habitat	Species	FR0	FR1	IV0	IV1	*p**	Group
RECENT	*Ox-Rhod*	*Dicr mont*	41	0	41	0	0.0308	Bryo
RECENT	*Ox-Rhod*	*Nowe curv*	49	0	49	0	0.016	Bryo
RECENT	*Ox-Rhod*	*Vacc viti*	90	100	32	64	0.0014	Vasc
RECENT	*Ox-Rhod*	*Pleu schr*	100	100	43	57	0.0108	Bryo
RECENT	*Ox-Rhod*	*Vacc myrt*	100	100	44	56	0.0034	Vasc
RECENT	*Ox-Rhod*	*Hylo sple*	100	100	46	54	0.0216	Bryo
RECENT	*Ox-Rhod*	*Pleu schr*	100	100	56	44	0.008	Bryo
RECENT	*Ox-Rhod*	*Hylo sple*	100	100	57	43	0.0002	Bryo
RECENT	*Ox-Rhod*	*Vacc myrt*	100	100	57	43	0.0002	Vasc
RECENT	*Ox-Rhod*	*Vacc viti*	100	88	65	31	0.0002	Vasc
RECENT	*Ox-Rhod*	*Luzu pilo*	90	84	56	31	0.0334	Vasc
RECENT	*Ox-Rhod*	*Mela prat*	90	69	65	19	0.0002	Vasc
RECENT	*Ox-Rhod*	*Conv maja*	70	53	50	15	0.0294	Vasc
RECENT	*Ox-Rhod*	*Rubu saxa*	55	34	44	7	0.0164	Vasc
CONSERV.	*Ox-Myrt*	*Hylo sple*	100	97	57	42	0.0458	Bryo
CONSERV.	*Ox-Myrt*	*Plag aspl*	56	79	13	61	0.0288	Bryo
CONSERV.	*Ox-Myrt*	*Soli virg*	89	50	60	16	0.0116	Vasc
CONSERV.	*Ox-Myrt*	*Mela prat*	100	47	76	11	0.0002	Vasc
CONSERV.	*Ox-Myrt*	*Mela sylv*	78	35	61	7	0.0018	Vasc
CONSERV.	*Oxalis*	*Rubu saxa*	85	100	36	58	0.0094	Vasc
CONSERV.	*Oxalis*	*Maia bifo*	96	100	41	57	0.0358	Vasc
CONSERV.	*Oxalis*	*Conv maja*	58	86	22	53	0.023	Vasc
CONSERV.	*Oxalis*	*Dryo cart*	96	83	57	34	0.0242	Vasc
CONSERV.	*Oxalis*	*Plag affi*	65	38	43	13	0.0348	Bryo
CONSERV.	*Oxalis*	*Stel holo*	73	38	49	12	0.0104	Vasc
CONSERV.	*Oxalis*	*Pter aqui*	27	72	8	51	0.004	Vasc
CONSERV.	*Oxalis*	*Orth secu*	8	34	2	27	0.0334	Vasc
CONSERV.	*Oxalis*	*Eurh angu*	58	28	41	8	0.023	Bryo
CONSERV.	*Oxalis*	*Dryo fili*	58	28	43	7	0.0124	Vasc
CONSERV.	*Oxalis*	*Plag elli*	46	17	34	4	0.0322	Bryo
CONSERV.	*Oxalis*	*Impa parv*	54	17	39	5	0.0116	Vasc
CONSERV.	*Oxalis*	*Stel nemo*	35	14	29	2	0.0488	Vasc
CONSERV.	*Oxalis*	*Urti dioi*	38	14	29	3	0.0336	Vasc

Appendix E

Species abbreviations list with corresponding Latin names.

Vascular Plants	
Abbervation	**Name**
Aego poda	*Aegopodium podagraria*
Anem nemo	*Anemone nemorosa*

Vascular Plants	
Abbervation	**Name**
Ange sylv	*Angelica sylvestris*
Athy fili	*Athyrium filix-femina*
Cala arun	*Calamagrostis arundinacea*
Call vulg	*Calluna vulgaris*
Care digi	*Carex digitata*
Care glob	*Carex globularis*
Care vagi	*Carex vaginata*
Conv maja	*Convallaria majalis*
Crep palu	*Crepis paludosa*
Daph meze	*Daphne mezereum*
Desc cesp	*Deschampsia cespitosa*
Desc flex	*Deschampsia flexuosa*
Dryo cart	*Dryopteris carthusiana*
Dryo expa	*Dryopteris expansa*
Dryo fili	*Dryopteris filix-mas*
Equi prat	*Equisetum pratense*
Equi sylv	*Equisetum sylvaticum*
Fest ovin	*Festuca ovina*
Frag vesc	*Fragaria vesca*
Gale lute	*Galeobdolon luteum*
Gali odor	*Galium odoratum*
Good repe	*Goodyera repens*
Gymn dryo	*Gymnocarpium dryopteris*
Hepa nobi	*Hepatica nobilis*
Impa parv	*Impatiens parviflora*
Lath vern	*Lathyrus vernus*
Luzu pilo	*Luzula pilosa*
Lyco anno	*Lycopodium annotinum*
Maia bifo	*Maianthemum bifolium*
Mela nemo	*Melampyrum nemorosum*
Mela prat	*Melampyrum pratense*
Mela sylv	*Melampyrum sylvaticum*
Mili effu	*Milium effusum*
Moeh trin	*Moehringia trinervia*
Moli caer	*Molinia caerulea*
Myce mura	*Mycelis muralis*
Orth secu	*Orthilia secunda*
Oxal acet	*Oxalis acetosella*
Pter aqui	*Pteridium aquilinum*
Pulm obsc	*Pulmonaria obscura*

Vascular Plants	
Abbervation	**Name**
Rubu idae	*Rubus idaeus*
Rubu saxa	*Rubus saxatilis*
Soli virg	*Solidago virgaurea*
Stel holo	*Stellaria holostea*
Stel nemo	*Stellaria nemorum*
Urti dioi	*Urtica dioica*
Vacc myrt	*Vaccinium myrtillus*
Vacc viti	*Vaccinium vitis-idaea*
Vero cham	*Veronica chamaedrys*
Viol rivi	*Viola riviniana*
Bryophytes	
Abbervation	**Name**
Brac oedi	*Brachythecium oedipodium*
Brac sale	*Brachythecium salebrosum*
Cirr pili	*Cirriphyllum piliferum*
Dicr hete	*Dicranum heteromalla*
Dicr maju	*Dicranum majus*
Dicr mont	*Dicranum montanum*
Dicr poly	*Dicranum polysetum*
Dicr scop	*Dicranum scoparium*
Eurh angu	*Eurhynchium angustirete*
Hylo sple	*Hylocomium splendens*
Hypn cupr	*Hypnum cupressiforme*
Loph hete	*Lophocolea heterophylla*
Nowe curv	*Nowellia curvifolia*
Plag aspl	*Plagiochila asplenioides*
Plag affi	*Plagiomnium affine*
Plag elli	*Plagiomnium ellipticum*
Plat curv	*Plagiothecium curvifolium*
Plat laet	*Plagiothecium laetum*
Pleu schr	*Pleurozium schreberi*
Poly comm	*Polytrichum commune*
Ptil cili	*Ptilidium ciliare*
Ptil pulc	*Ptilidium pulcherrimum*
Ptil cri-c	*Ptilium crista-castrensis*
Rhiz punc	*Rhizomnium punctatum*
Rhod rose	*Rhodobryum roseum*
Rhyt triq	*Rhytidiadelphus triquetrus*

Bryophytes	
Abbervation	**Name**
Sani unci	*Sanionia uncinata*
Spha girg	*Sphagnum girgensohnii*
Spha russ	*Sphagnum russowii*
Tetr pell	*Tetraphis pellucida*

Appendix F

pNDMS Figure without site type and region effect.

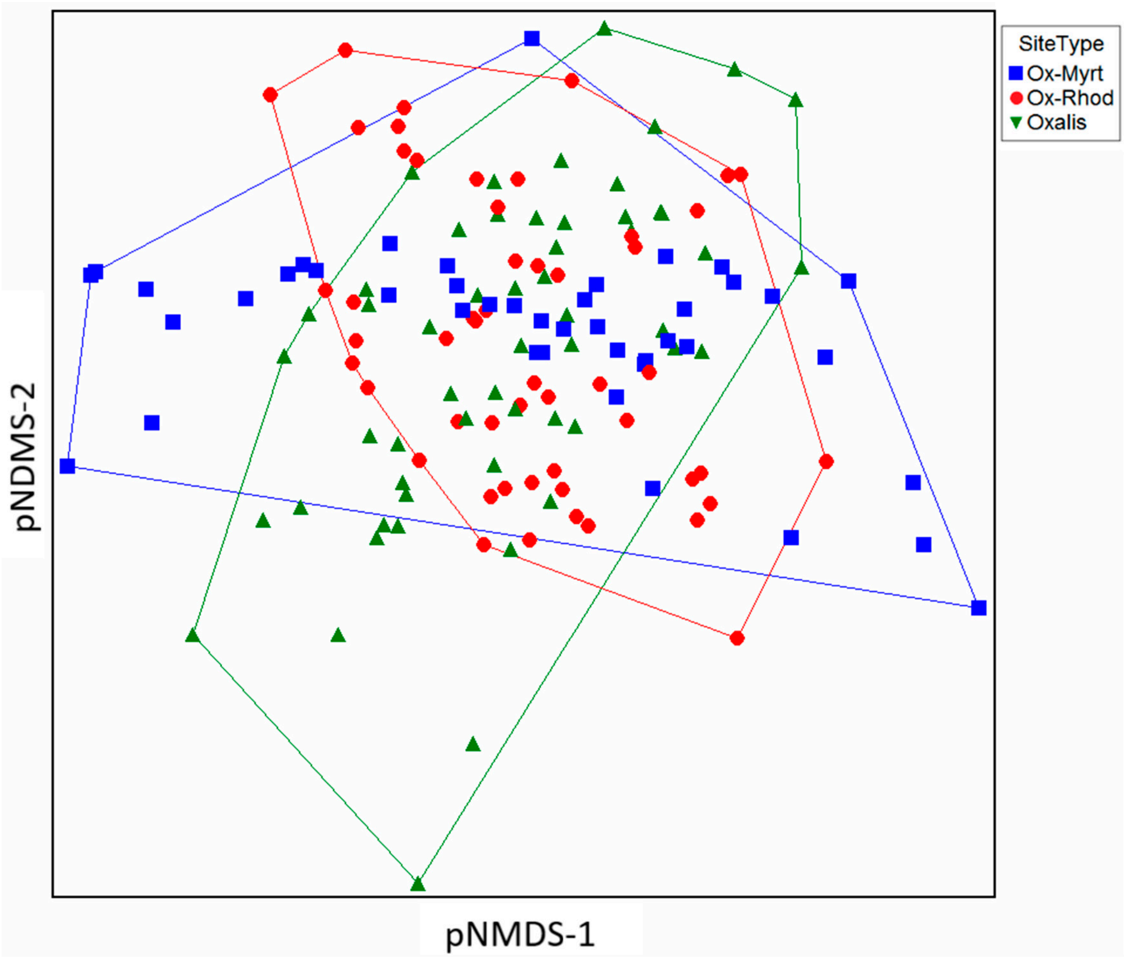

Figure A1. First (40% of variance, p = 0.004) and second (23% of variance, p = 0.004) axes of the pNDMS varimax ordination for 150 sample plots (final stress= 17.49488) using vascular plants and bryophytes logarithm residuals data without site type and region effect with species frequency > 3 on plot (n = 204) and 25 environmental variables (App 3). The plots are classified after site type (blue—*Ox-Myrt*, red—*Ox-Rhod*, green—*Oxalis*).

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