12th INTERNATIONAL SCIENTIFIC CONFERENCE
RURAL DEVELOPMENT 2025
RESILIENCE TO GLOBAL CHANGE
1-3rd October, 2025, Vytautas Magnus University Agriculture Academy, Lithuania

VYTAUTAS MAGNUS UNIVERSITY AGRICULTURE ACADEMY

Proceedings of the 12th International Scientific Conference Rural Development 2025

Edited by assoc. prof. dr. Judita Černiauskienė

ISSN 2345-0916 (Online)

Article DOI: https://doi.org/10.15544/RD.2025.032

PROTECTED LIVERWORT *ODONTOSCHISMA DENUDATUM* (MART.) DUMORT. COVER IS DEPENDENT ON MICROCLIMATE AND FOREST STAND AGE IN SOUTH-CENTRAL LATVIA CONIFEROUS FORESTS: CASE STUDY

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Sustainable species conservation and forest management are increasingly topical under increasing demand for forest related products, hence detailed knowledge about protected species ecology for multipurpose forestry. Bryophytes, particularly liverworts are excellent indicators of forest quality and they are significant part of biodiversity. The aim of our study was to understand protected liverwort *Odontoschisma denudatum* ecology in relation to substrate and forest stand scale variables in coniferous forests in Latvia. We studied *O. denudatum* on 25 dead logs that varied in diameter, decay class, length, height above ground, microtopography, stand age and area. We found that *O. denudatum* cover is higher in medium decay class and in older forest stands. Hence, the observed relationships suggest that the liverwort species is rather tolerant to studied variables within the stands it is present, upscaling of the study is still needed. We recommend also future monitoring of *O. denudatum* populations to follow up the species dynamics.

Keywords: *Odontoschisma denudatum*; liverwort; bryophyte; dead wood; epixylic; coniferous forests.

INTRODUCTION

While our knowledge about protected species occurrences are increasing, we are still missing information about their ecological conditions in forest ecosystems (Critchlow et al., 2022; Bellis et al., 2024). Bryophytes, particularly liverworts are excellend indicators of forest quality and they are significant part of biodiversity (Ek et al., 2002; Mežaka et al., 2022; Wang et al., 2025). Epixylic bryophytes play an important role in forest biodiversity (Wang et al., 2025). Many rare epixylic bryophyte species can be found on dead logs and ecology of these bryophytes are still poorly known (Laaka-Lindberg, 1999; Ek et al.; 2002). Among these species are also rare bryophyte species as *Odontoschisma denudatum* (Ek et al., 2002). This species is woodland key habitat indicator spcies (Ek et al., 2002) and grouped into a category of "least concerned" in the European Red List (Hodgetts & Lockhart, 2020). In Latvia *O. denudatum* is protected by national regulations as microreserve species (LRMK, 2012) and specially protected species (LRMK, 2000).

The latest study about epixylic liverwort *Odontoschisma denudatum* (Bambe et al., 2023; Bambe et al., 2024) in old-growth coniferous forests in Latvia showed that species cover was dependent on log length, forest stands above 100 years and forest stand area. The forest stand age is well known important driver in liverwort species richness (Crites & Dale, 1998) and composition (Rajandu et al., 2009). Also later decay stage of dead wood is important driver in liverwort colony establishment in Finland (Laaka–Lindberg, 2000). The number of epixylic bryophyte species was increasing with wood decay stage in *Picea abies* dominating forests in Sweden (Andersson & Hytteborn 1991).

Less is known about microclimatic and microtopography related variables in epixylic liverwort distribution (Noualhaguet et al., 2023). For rare epixylic bryophyte distribution particular role plays permanent humidity and shadow in coniferous forests (Laaka, 1992).

Study about epixylic bryophyte communities showed that they are highly dependent on humidity related microclimate in Czech Republic (Táborská et al., 2020). Microtopography can also serve as a refugia for forest floor bryophytes in managed forests (Schmalholz & Hylander, 2011). The aim of the present study was to characterize the *O. denudatum* cover in relation to substrate and forest stand scale variables in coniferous forests of South-Central Latvia. The study task was to find out the significant dead log and forest stand variables that are influencing *O. denudatum* cover in studied coniferous forest sites.

RESEARCH METHODS

Field work

The studied stands were located in four sites of south-central part of Latvia (Figure 1). Annual average air temperature in study sites are around +7^{o} C, annual rainfall is around 650 mm (LVĢMC, 2025). The studied sites are located in highly managed landscape in Latvia, where historically broad-leaved forests were cut down due to the agricultural purposes due to the fertile soils in the region. Most of the old – growth forest stands in this region are scattered across moderately forested landscape.

In total we selected four coniferous forest study sites (18 forest stands), where *Odontoschisma denudatum* (Figure 2) was found before according the National Natural Data Management system OZOLS and JSC Latvian State Forests databases. *Pinus sylvestris* and

Picea abies were dominant tree species in selected forest stands. We measured *O. denudatum* cover (cm^2) in a location on a log, where was the largest continuous patch. We selected 1-3 logs (depending on the size of the patch and presence of *O. denudatum*) per forest stand (in total 25 logs). We selected logs based on the previous records, where *O. denudatum* was found before based on National Natural Data Management system OZOLS.

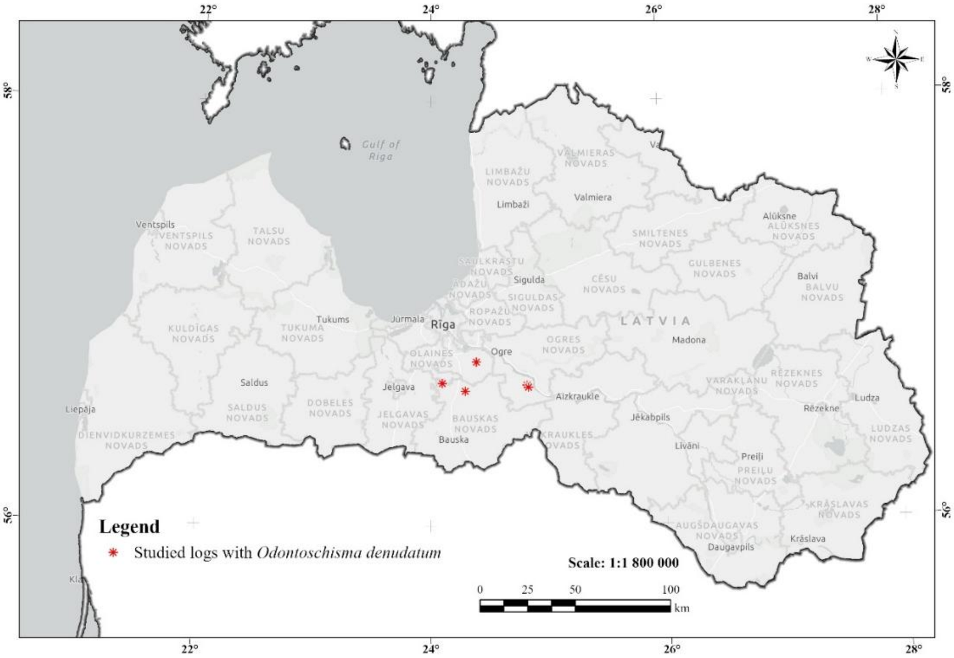

Figure 1. Studied sites (red asterisks). (map by Māris Nitcis).

Figure 2. *Odontoschisma denudatum* with gemmae on dead log in study site (photo by Edgars Dubrovskis).

We measured each log diameter (in a location, where *O. denudatum* was studied), length, decay class, microtopographical variables - microtopography (contour line) and *O. denudatum* height till vegetation (refers to height from studied *O. denudatum* population on a log (population central point) to the ground). Data about forest stand area and age were obtained from Latvian State Forest Service database.

For decay class of the log we applied modified log decay classes of C. Pyle and M.M. Brown (1998), where we joined classes and re-defined I, II, IIA as little decayed wood, III as medium decayed wood, IV and V as very decayed wood (Supplement material). Microtopography was evaluated based on contour lines (a countour/isoline is a line drawn on a map that joins points of equal height above sea level). Microtopography data were obtained from Latvian Geospatial Information Agency.

Data analysis

To identify variables (log diameter, log length, log decay class, microtopography, height to understorey vegetation, forest stand age and area) that are significant predictors of *O. denudatum* cover, we applied GLMM (Generalized linear mixed model) with glmmTMB function and Gaussian family that is suitable for continuous data. Random effect was a site. Each model fit was evaluated also graphically and with residuals. Data analysis was conducted in R programme, packages: 'lme4', glmmTMB, DHARMa (R Core team, 2021; Bates, 2015; Bolker, 2025; Hartig, 2024).

RESULTS AND DISCUSSION

Each studied log with *O. denudatum* was found in a depression that was evaluated during the field work in a forest and all sites were part of a bigger forest patch (not one isolated forest stand, but as a part of forest consisting of many connected forest patches). Studied *O. denudatum* population cover varied 5-15000 cm^2 (Supplement material). Average studied log diameter was 0.16 m, average log length: 13.30 m, average *O. denudatum* height till understorey vegetation – 0.20 m. Studied forest stand age varied 84–156 years and area: 0.44-4.50 ha. The average microtopography (contour line) of studied logs was 39.66 m (Supplement material).

The refined model showed that only dead log decay class and forest stand age were significant predictors of *O. denudatum* cover (Table 1). The lowest *Odontoschisma denudatum* cover was found on logs with little decay, while the highest cover was found on logs with medium decay class (Figure 3) similar as in earlier study in north west Latvia (Mežaka et al., 2022). Many liverworts were associated to middle stage of dead wood decay also in Canadian aspen mixed coniferous forests (Crites & Dale, 1998).

Table 1. *Odontoschisma denudatum* cover in relation to studied variables. Generalized linear mixed model results using glmmTMB function with Gaussian family and Site as a random factor. Height till vegetation refers to height from studied *O. denudatum* population on a log (population central point) to the ground.

Variables	Estimate	Std. Error	z-value	p
(Intercept)	-12336.5	5004.15	-2.47	0.01 *
Log length	55.59	173.22	0.32	0.75
Log diameter	1146.66	12152.91	0.09	0.93
Log_decayMedium	7149.92	3017.34	2.37	0.02 *
Log_decayVery	3340.1	2652.31	1.26	0.21
Height till vegetation	8083.99	11364	0.71	0.48
Stand age	63.51	30.64	2.07	0.04 *
Stand area	-1052.19	678.63	-1.55	0.12
Microtopography	-3.55	56.24	-0.06	0.95

In spite of some outliers, our data shows *O. denudatum* cover increase with a forest stand age (Figure 4). In other study in Canada epixylic bryophyte species richness was highest in older aspen forest stands (Crites & Dale, 1998). Similar to study by Rajandu et al. (2009), where coniferous forest stand age was significant predictor of log bryophyte vegetation. *Odontoschisma denudatum* population will have more time to form larger cover on logs with more time. Our results show that especially older forest stands are important for larger *O. denudatum* population long-term conservation. Similar conclusion was done also in earlier study by A. Mežaka et al. (2022).

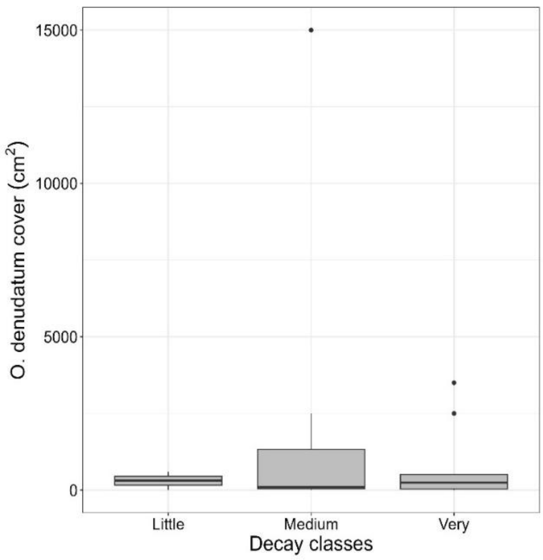

Figure 3. The cover of *Odontoschisma denudatum* cover in relation to dead log decay class. Plotted empirical data values.

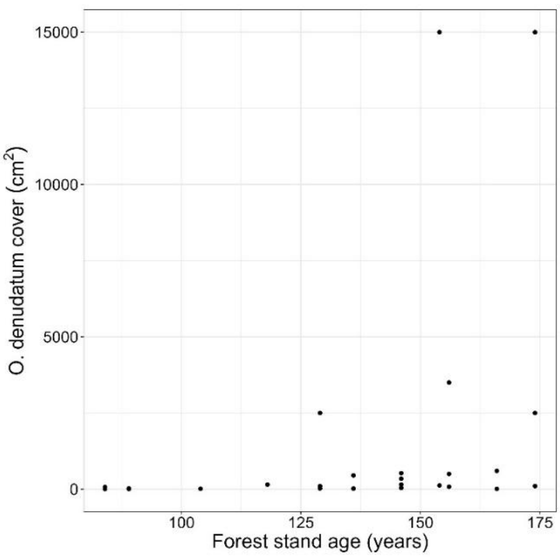

Figure 4. The cover of *Odontoschisma denudatum* cover in relation forest stand age. Plotted empirical data values.

Although we studied only 25 logs, our results could indicate that forest continuity that is provided by the time needed to colonize together with substrate are important predictors of *O. denudatum* cover. We assume that *O. denudatum* rarity is related to both: time and log in specific decay stage. Although, microtopography varied among studied logs, all of them were located in depression in a particular forest stand (not on a hill or visible elevation with studied forest stand). This could explain, why we did not find important humidity related factors (as height till vegetation) in a log scale significant in our analysis. This also could show that *O. denudatum* grows mostly only in these depressions, but more empirical data in Latvia are needed for conclusions.

In a future we recommend to initiate monitoring of *O. denudatum* populations on logs that will allow to follow dynamics of this species. We are also lacking a knowledge about *O. denudatum* population tolerance to changed environment, as distance to the clearcut.

CONCLUSIONS

Our results indicate that the cover of *O. denudatum* is dependent on substrate scale variable: dead log decay class and on forest stand scale variable: stand age. Other microclimatic conditions did not show significant influence on *O. denudatum* cover. Our population evaluation of *O. denudatum* (5-15000 cm^2) shows that species is in good condition on studied logs. This indicates that *O. denudatum* overall population in south central part of Latvia has a potential of long-term existence in older coniferous forest stands.

Acknowledgements. The study was financially supported by National Research Programme's "Research and Sustainable Use of Local Resources for the Development of Latvia 2023-2025" project No. VPP-ZM-VRIIILA-2024/2-0002 "Innovation in Forest Management and Value Chain for Latvia's Growth: NewForest Services, Products and Technologies (Forest4LV)". Thanks to Māris Nitcis for help with mapping. Thanks to Roberts Matisons for valuable comments about this study.

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Supplement material. Studied variable characteristics of each sample log. Height till vegetation refers to height from studied *O. denudatum* population on a log (population central point) to the ground.

Sample	*O. denudatum* cover (cm^2)	Log length (m)	Log diameter (m)	Log decay class	Height till vegetation (m)	Age (years)	Area (ha)	Latitude	Longitude	Contour line (m)
K1	2500	15.80	0.29	Medium	0.30	129	2.95	56.6718	24.0986	10.12
K2	25	18.50	0.20	Medium	0.20	129	2.95	56.6717	24.0987	10.09
K3	100	8.50	0.15	Medium	0.13	129	2.95	56.6719	24.0984	10.09
K4	150	12.60	0.21	Medium	0.24	118	4.5	56.6716	24.09782	10.03
K5	100	8.70	0.11	Medium	0.21	174	1.84	56.6353	24.29363	26.68
K6	2500	19.30	0.18	Very	0.37	174	1.84	56.6355	24.29348	26.62
K7	15000	15.90	0.10	Medium	0.36	174	1.84	56.6356	24.29337	26.83
K8	6	4.30	0.10	Very	0.12	89	0.85	56.6349	24.29392	27.66
K9	25	15.50	0.23	Very	0.23	89	0.85	56.6348	24.29338	27.56
K10	70	3.85	0.05	Medium	0.08	84	1.37	56.6344	24.29313	28.22
K11	12	13.40	0.14	Medium	0.16	104	1.31	56.7722	24.39172	32.65
K12	5	12.90	0.16	Medium	0.11	84	1.82	56.7722	24.39101	32.54
K13	120	5.00	0.13	Very	0.14	154	0.74	56.7713	24.39085	32.77
K14	15000	10.00	0.21	Medium	0.19	154	0.74	56.7713	24.38999	32.76
K15	20	20.00	0.16	Very	0.17	136	1.68	56.6634	24.82251	57.58
K16	450	3.00	0.11	Very	0.29	136	0.59	56.6633	24.82419	57.13
K17	600	15.50	0.05	Little	0.16	166	1.17	56.663	24.82426	57.11
K18	152	13.40	0.05	Very	0.12	146	0.86	56.6628	24.82317	58.83
K19	343	18.00	0.32	Very	0.30	146	0.86	56.6624	24.82373	58.02
K20	9	20.50	0.23	Little	0.25	166	1.07	56.6621	24.82363	57.80
K21	3500	20.30	0.23	Very	0.20	156	3.41	56.6548	24.83182	61.49
K22	500	14.30	0.08	Very	0.19	156	0.44	56.6521	24.83475	62.16
K23	525	15.50	0.21	Very	0.23	146	4.26	56.6512	24.83286	62.19
K24	40	12.80	0.15	Very	0.20	146	2.1	56.6514	24.83478	62.24
K25	80	14.90	0.15	Medium	0.0002	156	1.58	56.6515	24.83487	62.23
Min	5	3	0.05		0.0002	84	0.44			22
Max	15000	20.5	0.32		0.37	174	4.50			76
Avg.	1673.28	13.30	0.16		0.20	137.64	1.78			51.20