The main drivers for the occurrence of six red-listed epiphytic bryophytes and lichens in the boreo-nemoral forest landscape, Latvia

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Abstract: Forest landscape plays a significant role in rare cryptogam distribution. However, data about the environmental demands of rare epiphytic bryophytes and lichens in boreo-nemoral forest landscapes are not complete. In this study, we focused on finding the main environmental predictors influencing the occurrence of three red-listed epiphytic bryophytes and three red-listed epiphytic lichens in the Latvian boreo-nemoral forest landscape. We obtained the records of species from the Natural Data Management System OZOLS database, which is a national information system on all rare taxa. We analyzed the occurrence of species in relation to forest stand age and area, forest type, heterogeneity and tree bark pH class. We found that selected red-listed bryophyte and lichen occurrence was mainly influenced by forest stand age and area. However, each of the red-listed epiphytic bryophyte and lichen has their own ecological demands in the boreo-nemoral landscape.

Keywords: cryptogams, rare taxa, database analysis, forest stand characteristics

INTRODUCTION

In total, 43% of all legally protected (term originated from the Latvian government with aim to list the species with a conservation concern) bryophyte species protected by governmental policies (LRMK, 2000), and 39% of all red-listed bryophyte species of Latvia are distributed in forests (Āboliņa, 1994; Liepiņa, 2017; Gerra-Inohosa, 2018). In the case of lichens, 82% of specially protected species (LRMK, 2000) and 65% of all red-listed lichenized fungi (lichens) in Latvia are related to forest habitats (Andrušaitis et al., 1996), where the vast majority (> 90%) are epiphytic lichens. This shows the importance of the forest landscape in bryophyte and lichen distribution and conservation. Measuring the alteration of forest habitats reveals the changes in the "living room" of these species groups.

Boreo-nemoral forest stand characteristics such as forest habitat type, forest stand age, forest stand area and number of tree species in a forest stand (heterogeneity; Cleavitt, 2005; Jüriado et al., 2009; Perhans et al., 2009; Caners et al., 2013; Nascimbene et al., 2013; Ódor et al., 2014) and pH of tree bark (Barkman, 1958; Gustafsson & Eriksson, 1995; Kuusinen, 1996; Sætersdal et al., 2005; Marmor et al., 2017) are important drivers influencing the distribution of epiphytic bryophytes and lichens in these forests, but there is insufficient understanding of how these predictors relate to particular rare epiphytic species (Hazell et al., 1998; Gustafsson et al., 2004; Löbel et al., 2006; Fedrowitz et al., 2012; Westerberg et al., 2017).

It has been known for decades that each species has its fundamental and realized niche that is highly dependent on the abiotic and biotic environment (Hutchinson, 1957). Despite the increasing number of studies on the ecology of epiphytic bryophytes and lichens, we still lack knowledge on optimal site condition for the rare bryophytes and lichens (Gustafsson et al., 1992; Snäll et al., 2004; Löbel et al., 2006; Ronnås et al., 2017). It is important to identify the key ecological variables that support the development of endangered species in a given area (Brown, 1995). Previous studies have shown that forest stand age has a significant effect on the occurrence of red-listed bryophyte species in both mature and managed forests in Sweden (Gustafsson et al., 2004), and the number of red-listed and indicator lichens of Woodland Key Habitats (WKH) in Swedish commercial forests was also higher in older forest stands (Johansson & Gustafsson, 2001). Therefore, the age of forest stand can be the main factor for the occurrence of epiphytic bryophytes and lichens in forest landscapes.

The aim of our study is to characterize the main drivers for the occurrence of selected red-listed

epiphytic bryophyte and lichen taxa in the boreo-nemoral forest landscape of Latvia based on available data from inventories, monitoring and other projects in Latvia from 2005 to 2020. The hypothesis of the study is: the highest occurrence of most of the selected epiphytic bryophyte and lichen taxa will be associated with older forest stands and with forest heterogeneity.

MATERIALS AND METHODS

Study site and objects

Latvian forest landscape typically consists of different forest patch mosaics alternating with agricultural land, which forms fragmented landscape. Today, forest cover is estimated at around 52% of the total area of Latvia. Most of the forest cover is formed by coniferous stands (52% of total forested area), where *Pinus sylvestris* L. and *Picea abies* (L.) H. Karst are dominating, while deciduous stand cover, dominated by various tree species (e.g., *Betula pendula* Roth.*, Alnus incana* (L.) Moench*, Populus tremula* L.), is smaller (State Forest Service, 2021). The climate in Latvia is characterized by an annual rainfall of 692 mm. The coldest month is February, with an average air temperature of −3.7° C. The warmest month in Latvia is July, with an average air temperature of +17.4° C (LVĢMC, 2021).

We selected the red-listed epiphytic bryophyte species: *Dicranum viride* (Sull. & Lesq.) Lindb.*, Neckera complanata* (Hedw.) Huebener and *Lejeunea cavifolia* (Ehrh.) Lindb.*,* and the lichens: *Cetrelia olivetorum* s. lat.*, Menegazzia terebrata* (Hoffm.) A. Massal. and *Thelotrema lepadinum* (Ach.) Ach. (Table 1). The selected species are WKH specialist. The status as WKH specialist indicates that the forest patch in which this taxa occurs corresponds to WKH (Ek et al., 2002). *Dicranum viride* is also listed in Annex II of EU Habitat Directive 92/43 (Council Directive 92/43/EEK, 1992). All selected species are also legally protected (LRMK, 2000). These six species were selected according to their rarity in Latvia (red-listed species (Āboliņa, 1994; Andrušaitis et al., 1996) or/and protection status by Latvian government (LRMK, 2000; LRMK, 2012), representing different morphology, growth forms and dispersal modes that may also cause different ecological requirements. Other detailed information about selected species is given in Table 1.

Data collection

For data analysis, we obtained data available from the Natural Data Management System OZOLS database by the request of the Nature Conservation Agency in Latvia. From OZOLS database, we selected species records registered by certified bryophyte and lichen experts who have appropriate experience in bryology and lichenology. It helped us to avoid records, where study species may be incorrectly identified.

We selected study sites in locations which have been well studied before in terms of bryophytes and lichens based on several inventories, monitoring and other projects in Latvia from 2005 to 2020 to avoid a false absence data problem (Lauriault & Wiersma, 2019). While we are aware of the probability of false absences in our data, their influence on our data is likely to be minor. The selected study sites were located in geographically diverse forest landscape areas in Latvia. We collected data in three steps: 1) site selection; 2) formation of sample plots; 3) random forest stand selection within a sample plot. Below we gave a description of each of the three steps in data collection.

In total we compiled data about three red-listed bryophyte and three red-listed lichen species in 30 sites in Latvia (five sites for each red-listed bryophyte and red-listed lichen species). We selected sites, where these species were the most abundant. Selected bryophytes and lichens have at least 15 records (one record correspond to occurrence in one forest stand) in the selected study sites. This selection helped us to obtain data that are enough for data analysis.

In each site we made a sample plot in size of 1x1 km. The sample plot was designed around the species records, the centre of the plot being where most of the records of the species were found. This approach helped us to simplify the data analysis, to standardize sampling and to show data about red-listed species occurrence on a landscape scale.

Each sample plot (1x1 km) consisted of different forest types and more than 30 forest stands. To standardize the data analysis, we selected randomly 30 forest stands in each 1x1 km sample plot (in total 150 forest stands for each selected red-listed bryophyte and lichen species). The random selection procedure of forest stands in

Table 1. Studied red-listed bryophyte and lichen taxa and their characteristics. Data compiled from the sources: Abolina (1968), Council Directive 92/43/EEK (1992), Āboliņa (1994), Andrušaitis et al. (1996), LRMK (2000), Ek et al. (2002), Motiejūnaitė (2005), Smith et al. (2009), Kukwa et al. (2012), LRMK (2012), Liepiņa (2017), Hodgetts et al. (2019), Mark et al. (2019), Degtjarenko & Moisejevs (2020), Hodgetts et al. (2020).

Species	Phorophyte	Dominant forest type	Red-listed status in Latvia	Red-listed status in Europe	Habitat directive Annexes	Protection by Latvian government policies and other materials
Dicranum viride	Deciduous, *Pinus sylvestris*	Slope and ravine, old deciduous	Rare	Least concern	II	LRMK, 2000, Ek et al., 2002
Lejeunea cavifolia	Deciduous	Slope and ravine, old deciduous, old boreal	Vulnerable	Least concern	-	LRMK, 2000; LRMK, 2012; Ek et al., 2002
Neckera complanata	Different tree species	Dry and wet deciduous, mixed tree	Vulnerable	Least concern	-	LRMK, 2000; Ek et al., 2002
Cetrelia olivetorum s. lat.	*Alnus* spp., *Fraxinus excelsior* L., *Tilia cordata* Mill.	Old-growth	Endangered	-	-	LRMK, 2000; LRMK, 2012; Ek et al., 2002
Menegazzia terebrata	*Alnus glutinosa* (L.) Gaertn*., Betula pubescens* Ehrh*., Tilia cordata, Picea abies, Populus tremula, Padus avium* L.	Old-growth shady	Rare	-	-	LRMK, 2000; LRMK, 2012; Ek et al., 2002
Thelotrema lepadinum	*Alnus* spp., *Quercus* spp., *Tilia* spp.	Old-growth shady	Rare	-	-	LRMK, 2000; LRMK, 2012; Ek et al., 2002

each sample plot (1x1 km) was based on the following criteria: 1) the selected red-listed taxa had been recorded in at least 3 forest stands within a sample plot; 2) the minimum age of the randomly selected forest stand is older than 2 years. All manipulations in data selection were done using programme Arc GIS pro version 2.7 (ArcGIS® software by ESRI).

Data analysis

To analyze the relationship between selected red-listed bryophyte and lichen occurrences and forest stand variables, we obtained data about forest stand characteristics from the Latvian Forest Resource Database (updated in 2020; Table 2). For each selected forest stand, we obtained information about forest stand age, forest stand area (the size of the forest patch), forest type (Latvian Forest Resource Database, modified after Kabucis (2001), Appendix 1) and heterogeneity (number of tree species in a forest stand tree layer, Appendix 1). We also evaluated

tree bark pH class based on the tree species composition; one of two categories for each forest stand based on the presence of "rich" or "poor" bark trees in a forest stand, modified by Barkman (1958) and Mežaka & Znotiņa (2006). Forest stand age is calculated of the tallest and with a higher wood volume tree species of the forest layer in a forest stand (data were obtained from the Latvian Forest Resource Database upon the official request). Heterogeneity refers to the number of the tree species in a tree layer of a particular forest stand. The forest stand condition (bark pH class) was based on the presence or absence of favourable tree species for cryptogam species richness (Hazell et al., 1998; Mežaka & Znotiņa, 2006). If a tree layer of the forest stand had at least one of the following species present, the bark pH class was "rich" or if absent – "poor": *Acer platanoides* L., *Alnus incana, Fraxinus excelsior, Populus tremula, Salix* sp., *Ulmus* sp.

Table 2. Drivers of forest characteristics. Forest type refers to six forest types: dry coniferous, dry deciduous, dry mixed tree, wet coniferous, wet deciduous, wet mixed tree. Heterogeneity refers to number of tree species in a forest stand tree layer. Bark pH class: P refers to the presence of tree species in forest stand with only "poor" or acidic bark; R refers to the presence of tree species in forest stand with "rich" or alkaline tree bark.

Drivers	Value range	Unit
Forest stand age	2-238	years
Forest stand area	0.10-22.75	ha
Forest type	1-6	forest type number
Heterogeneity	1-5	tree species number
Bark pH class	P, R	"poor" or "rich"

To understand the main drivers of selected red-listed taxa occurrence in the forest landscape in Latvia, we related the forest stand variables: forest stand age, forest stand area, forest type, heterogeneity and bark pH class (Table 2) with selected red-listed taxa occurrence, applying the generalized linear model (GLM; Zuur et al., 2009) with binomial family. To understand, if taxa occurrence is driven by forest stand age dependent on forest type and if taxa occurrence is driven by forest stand age dependent on heterogeneity, we added two interaction terms in GLMs as potential predictors: forest stand age x forest type and forest stand age x heterogeneity.

Continuous variable in interaction terms were mean-centered to make interaction comparable with other variables in a model. We started GLM with a full model (all potential predictors) and the best GLMs were selected using backward stepwise selection based on the results of a likelihood ratio test. We removed one predictor which was not significant in each backward stepwise selection step. We applied a coefficient of partial determination (R^2) to calculate the proportion variation explained by each predictor in a final model (Zhang, 2017). The significance of each variable was calculated with ANOVA function from 'car' package. The R^2 was calculated using 'rsq' package (Zhang, 2021). Data analysis was conducted in R programme version 4.0.3 (R Core Team, 2020).

RESULTS

The total number of study species records was 122 (Table 3). The most common was *N. complanata* and *T. lepadinum*. Both of these species were the most frequent in dry mixed forests and next common forest type for these species was dry deciduous forest. Liverwort *L. cavifolia* had wide gradient in terms of forest type; it was found in five forest types, from dry coniferous forest to wet mixed tree forest. *Dicranum viride* and *C. olivetorum* were found only in three forest types: dry deciduous, dry mixed tree and wet deciduous. Almost half of the records of *M. terebrata* were found in dry mixed forests. We did not find any selected red-listed taxa records in wet coniferous forests.

Table 3. Taxa frequency in studied forest types.

Species	Forest types						Percentage of all records
	Dry coniferous	Dry deciduous	Dry mixed tree	Wet coniferous	Wet deciduous	Wet mixed tree	
Bryophytes	Percentage of the particular species records						
Dicranum viride	-	72.2	16.7	-	11.1	-	14.8
Lejeunea cavifolia	20.0	35.0	25.0	-	5.0	15.0	16.4
Neckera complanata	8.7	43.5	43.5	-	4.4	-	18.9
Lichens							
Cetrelia olivetorum	-	56.3	37.5	-	6.3	-	13.1
Menegazzia terebrata	-	28.6	47.6	-	9.5	14.3	17.2
Thelotrema lepadinum	-	29.2	50.0	-	16.7	4.2	19.7

Table 4. Generalized linear models (GLMs) of red-listed bryophyte and lichen occurrences and studied variables. The number of tree species in a stand refers to heterogeneity. R^2 refers to coefficient of partial determination.

Response	Predictors	Statistics		
		R^2	Residual of deviance	p
Dicranum viride	Forest stand age	0.19	89.43	<0.01
	Forest stand area	0.25	67.29	<0.01
	Bark pH class	0.06	61.07	<0.01
Lejeunea cavifolia	Forest type	0.09	113.77	0.54
	Forest stand age	<0.01	96.23	<0.01
	Forest stand area	0.21	86.67	<0.01
	Heterogeneity	0.07	84.73	0.16
	Bark pH class	0.15	73.47	<0.01
	Forest type: Forest stand age	0.14	60.23	0.02
	Heterogeneity: Forest stand age	<0.01	58.90	0.25
Neckera complanata	Forest stand age	0.22	100.4	<0.01
	Bark pH class	0.05	93.82	0.01
Cetrelia olivetorum	Forest stand age	0.12	78.89	<0.01
Menegazzia terebrata	Forest stand age	0.28	91.10	<0.01
	Forest stand area	0.15	78.70	<0.01
Thelotrema lepadinum	Forest type	0.11	117.95	0.02
	Forest stand age	0.13	104.40	<0.01

The GLM analysis revealed that occurrence of all selected red-listed bryophytes and lichens increased significantly with forest stand age (Table 4, Appendix 2). Furthermore, forest stand age was the only significant predictor of the occurrence of *C. olivetorum* (Table 4). Most of the studied taxa showed a rapid increase in probability of taxa occurrence starting in 100-year-old forest stands (Appendix 2). The frequency of *L. cavifolia* was influenced significantly by forest type and forest stand age interaction, where the probability of having *L. cavifolia* was rapidly increasing in older dry coniferous and wet deciduous forest stands. Forest type was also significant for *T. lepadinum* occurrence (Table 4), where the highest probability of having this species was in dry mixed tree forests.

The set of the significant variables in a final GLM differed among the studied taxa. Probability of having each of the studied bryophyte species increased significantly with having "rich" bark trees in forest stands (Table 4, Appendix 2, C, F, H). Forest stand area was significant in *D. viride*, *L. cavifolia* and *M. terebrata* frequency (Table 4), and the probability of having these species increased with forest stand age (Appendix 2, B, E, K).

DISCUSSION

Our results only partly support our hypothesis that occurrence of rare species will be associated with forest stand age, forest stand area and number of tree species in forest stands. While each selected red-listed species presence is associated to forest stand age, only *D. viride*, *L. cavifolia* and *M. terebrata* is associated with forest stand area. Heterogeneity has no significant effect on any selected species occurrence (Table 4).

Forest stand age is related to the natural state of the forest and also may indirectly reflect the historical management of the forest (Fritz et al., 2008; Moning et al., 2009; Wierzcholska et al., 2020). The older forest stands have more preferable quality of tree bark substrate (Kuusinen & Penttinen, 1999; Humphrey et al., 2002; Johansson et al., 2007) and more time

than younger forest stands for successful rare species dispersal and colonization (e.g., the probability that propagule will reach the suitable substrate is higher in longer time intervals than shorter time intervals in general).

We speculate that many rare species are more susceptible to microclimatic conditions in a particular forest stand than common species. These microclimatic conditions in terms of environmental filtering might indirectly influence species dispersal abilities (for example, producing smaller amount of propagules) and propagule establishment among forest stands. Similarly, a study of boreal forests in Sweden shows that microclimatic differences among large and small forest patches are important for several epiphytic species (Perhans et al., 2009). Forest stand area was important in epiphytic bryophyte species dispersal in fragmented boreo-nemoral forest landscape in Sweden (Löbel et al., 2006), while epiphytic lichen was not dispersal limited in the mountain landscape of Central Europe (Werth et al., 2006).

Species dispersal is highly important in metapopulation processes. Metapopulation structure is also common in epiphyte communities (Löbel et al., 2006), and the patch-tracking metapopulation theory was suggested for epiphytic cryptogams (Snäll et al., 2003), which postulates that epiphytes will stay on a tree until the tree will fall down. This shows the importance of a suitable forest stand area in metapopulation dynamics. In this setting, due to restricted dispersal and tree-fall, epiphytic species will become extinct (Löbel et al., 2006) if there is not a suitable patch or substrate for epiphyte propagule colonization.

Our results show that *D. viride*, *L. cavifolia* and *M. terebrata* were associated with forest stand area. These species were probably maintaining local metapopulations with limited dispersal ability. Evidence showed that bryophyte asexual propagules can disperse only several centimeters from the source plant and maintain mostly local populations (Laaka-Lindberg et al., 2003). This can be true for bryophyte *D. viride* and lichen *M. terebrata* in our study because these species produce asexual propagules which could have difficulties passing unsuitable patches (such as clear-cuts) before establishment on suitable substrate. A complete understanding of epiphytic bryophyte

and lichen dispersal abilities is still lacking. Many bryophyte species showed dispersal ability exceeding 100 km in woodlands of Netherlands (Bremer & Ott, 1990), but the authors did not reveal if this dispersal was with spores or with asexual propagules. A recent study of Central European broadleaved and coniferous forests showed that the lichens *M. terebrata* and *C. olivetorum* have dispersal limitations (Dymytrova et al., 2018). Epiphytic lichen distribution and abundance was explained by local dispersal and environmental filtering in Norwegian deciduous forests (Schei et al., 2012).

The lack of the importance of heterogeneity in the studied red-listed species could be explained by the rare epiphytic species specialization to specific tree species, and the tree species diversity in a forest stand may not be important. Other studies showed that epiphytes are confined to particular tree species (Barkman, 1958, Ranlund et al., 2018, Liira et al., 2020).

Our study shows that each of the selected epiphytic bryophytes and lichens have their specific relationships with studied predictors. For instance, only *L. cavifolia* and *T. lepadinum* showed an association with forest type. Bryophytes and lichens showed a significant relationship with forest habitat type in the Białowieża forest (Czerepko et al., 2021), but a low degree of habitat specialization was found for epiphytic bryophytes in boreo-nemoral forests in Sweden (Löbel et al., 2006). The Białowieża forest is a nemoral forest, but we studied the boreo-nemoral forests; this indicates that these forests may not be comparable. Local scale variables, such as substrate tree availability, may be more important than habitat type for other rare epiphytic bryophytes and lichens in the Latvian forest landscape.

Surprisingly, while the presence of "rich" bark tree species in the studied forest stands is significant and has positive effects for all rare bryophyte species and it is not significant for occurrence of selected lichen species in our study. However, evidence that rare lichen *Menegazzia terebrata* can grow on both deciduous and coniferous tree species (Andrušaitis et al., 1996) with different bark pH can explain our results. Experimental results showed that substrate pH is important in rare bryophyte propagule germination (Wiklund &

Rydin, 2004; Löbel & Rydin, 2010) and also for the growth of both rare and common moss species fragments (Cleavitt, 2001). A study in Estonia showed that tree bark pH is important for red-listed epiphytic lichen occurrence (Marmor et al., 2017). We could speculate that if our study had included all rare epiphytic lichen species in Latvia, the importance of tree bark pH would probably have been shown to be significant for several lichens

CONCLUSIONS

Our study shows that forest characteristics such as forest stand age and area are important drivers for the occurrence of rare epiphytic bryophytes and lichens in the Latvian forest landscape. Tree bark pH class is important driver in rare epiphytic bryophyte species occurrence. Selected epiphytic bryophytes and lichens have their own ecological requirements in the boreo-nemoral forest landscape. The next step in future studies is to apply species niche modeling approaches (Wierzcholska et al., 2020) to predict and analyze the distribution patterns of rare bryophytes and lichens in Latvia.

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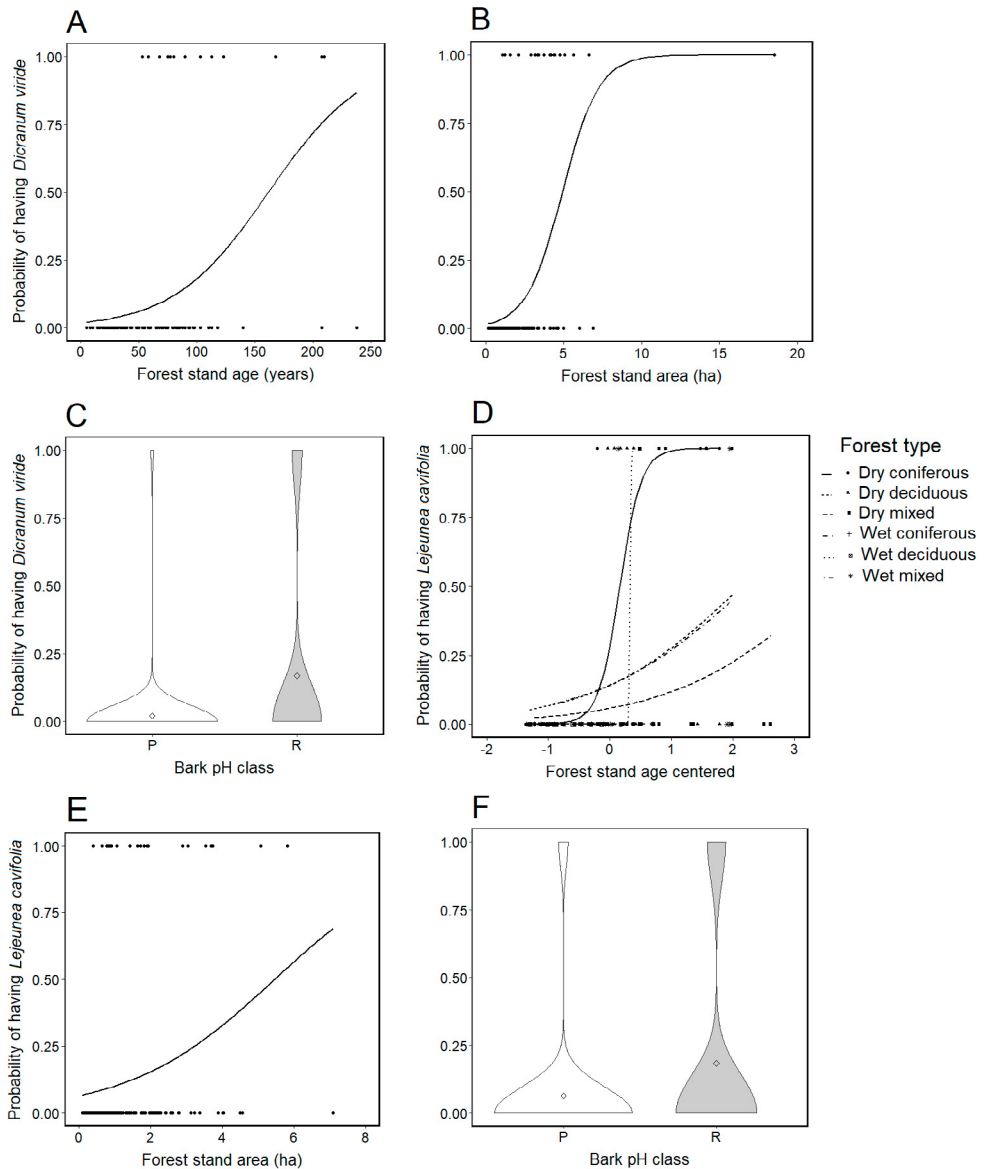
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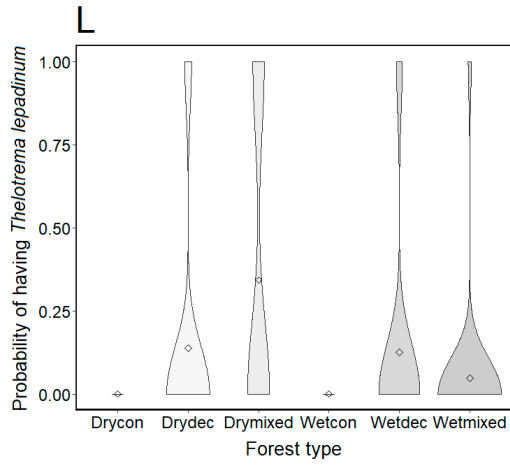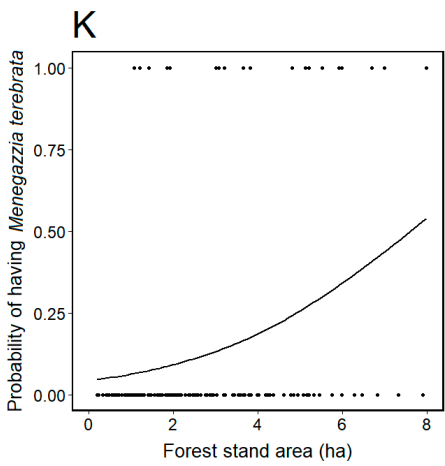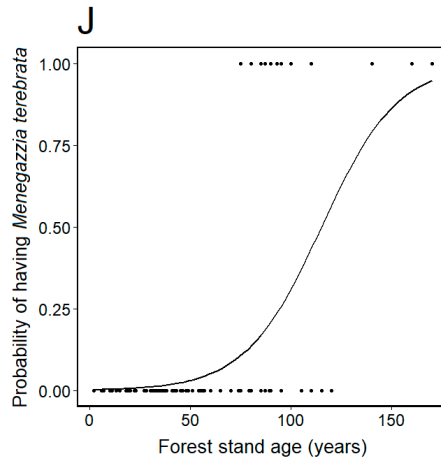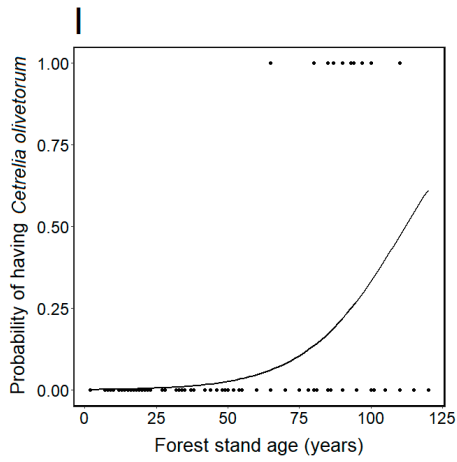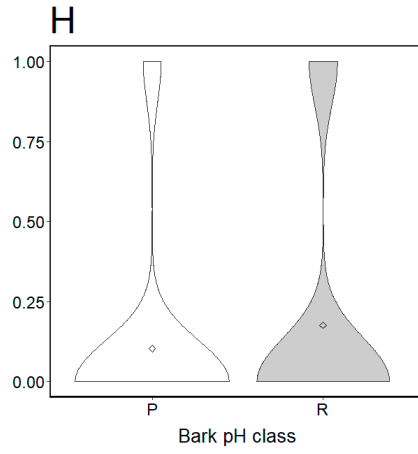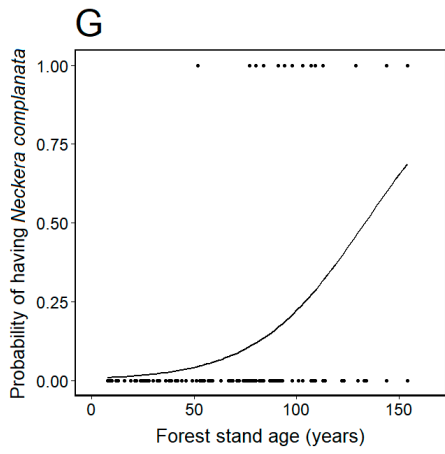
Appendix 1. Studied forest types and tree species. Ag: *Alnus glutinosa* (L.) Gaertn., Ai: *Alnus incana* (L.) Moench, Ap: *Acer platanoides* L., Bp: *Betula pendula* Roth, Fe: *Fraxinus excelsior* L., Pa: *Picea abies* (L.) H. Karst, Ps: *Pinus sylvestris* L., Pt: *Populus tremula* L., Qr: *Quercus robur* L., Sc: *Salix caprea* L., Ssp; *Salix* sp., Tc: *Tilia cordata* Mill., U: *Ulmus* sp.

Forest type	Tree species													Total number of tree species
	Ag	Ai	Ap	Bp	Fe	Pa	Ps	Pt	Qr	Sc	Ssp	Tc	U	
Dry coniferous		1		1	1	1	1	1	1			1		8
Dry deciduous	1	1	1	1	1		1	1	1	1	1	1	1	12
Dry mixed tree	1	1		1	1	1	1	1	1	1		1		10
Wet coniferous	1					1	1							3
Wet deciduous	1	1	1	1	1			1	1	1	1	1	1	11
Wet mixed tree	1	1		1	1	1	1		1					8

Appendix 2. Fitted (lines) values of GLM and observed values (dots) of red-listed epiphytic occurrence (probability of having species) of bryophytes and lichens in relation to studied variables. Open points in violin plots refer to mean values. Bark pH class: P refers to the presence of tree species in forest stand with only "poor" or acidic bark; R refers to the presence of tree species in forest stand with "rich" or alkaline tree bark. Shown are only significant predictors of GLMs. Probability of having *Dicranum viride* in association to forest stand age (A), forest stand area (B) and bark pH class (C). Probability of having *Lejeunea cavifolia* in association to interaction forest type x forest stand age (mean centered) (D), forest stand area (E) and bark pH class (F). Probability of having *Neckera complanata* in relation to forest stand age (G) and bark pH class (H). Probability of having *Cetrelia olivetorum* in relation to forest stand age (I). Probability of having *Menegazzia terebrata* in relation to forest stand age (J) and forest stand area (K). Probability of having *Thelotrema lepadinum* in relation to forest type (L) and forest stand age (M).

Appendix 2 (cont.).

Appendix 2 (cont.).