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Tree regeneration in noble broadleaved tree stands at their northern limit: implications for conservation management

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Abstract

In Latvia, the noble broad-leaved tree species woodland with pedunculate oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.), Norway maple (*Acer platanoides* L.), wych elm (*Ulmus glabra* Huds.), white elm (*Ulmus laevis* Pall.) and common ash (*Fraxinus excelsior* L.) has decreased to about 1% due to the historical legacy of wood extraction and conversion of fertile soil to agricultural land-use. The aim of the current study was to determine the tree age structure in the canopy and size structure in the shrub layer of broad-leaved tree stands to determine past changes and to predict future trends in tree species composition in the context of potential management methods. In 50 randomly selected broad-leaved tree stands, plots of size 0.1 ha were established. In the plots, diameter at breast height was measured for all trees with diameter >10 cm and cores were removed from all of these trees. All other stems were counted by species in height classes ≤ 1 m, 1.1 to 5 m, 5 to 10 m. The stands were classified into 10 groups based on canopy composition in age classes. Norway spruce [*Picea abies* (L.) H. Karst.] was common in various tree layers of in many of the groups, and it is recommended that it should be removed during stand tending. *Q. robur* regeneration should be promoted in specific cases where abundant in the < 1 m layer and where large gaps can be created. *T. cordata* is commonly present in several tree layers and its growth could be promoted by thinning of *P. abies* where present. Abundant *Q. robur* regeneration is sometimes found in Scots pine (*Pinus sylvestris* L.) stands.

Key words: broadleaved forests, conservation management, tree regeneration.
Abbreviations: DBH, diameter at breast height.

Introduction

In the boreo-nemoral zone (Sjörs 1963) in Latvia, the noble broad-leaved tree species pedunculate oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.), Norway maple (*Acer platanoides* L.), wych elm (*Ulmus glabra* Huds.), white elm (*Ulmus laevis* Pall.) and common ash (*Fraxinus excelsior* L.) occur close to their northern distribution limit (Ozenda 1994). European hornbeam (*Carpinus betulus* L.) has been successfully planted in a few locations in Latvia, which are far north of its natural range. The total area of woodland dominated by these noble broad-leaved tree species is small; the total forest area is 55%, of which only about 1% is dominated by broad-leaved tree species, mostly oak. In the general boreal landscape, these stands have great value in conservation due to the typical nemoral vegetation and epiphytic lichen and bryophyte diversity. However, predicted tree range shifts under climate change scenarios suggest that by 2100 in the present boreo-nemoral zone, dominance of tree species composition by conifers Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) H. Karst.] will be replaced by the broad-leaved tree species (Hanewinkel et al. 2013). These range shifts are likely to be promoted by a CO_2 fertilization effect on productivity (Lindner et al. 2010).

Q. robur is a common tree species of the temperate zone on a range of soil types, with preference for more basic, rich and heavy soils, but also can be found on poor dry as well as wet soils (Jones 1959). Associated tree species are *Ulmus, Fraxinus, Acer* and *Carpinus* (Johnson et al. 2002). *Q. robur* possesses traits of a pioneer species, like *P. sylvestris* and European aspen (*Populus tremula* L.), and requires well sunlit conditions for regeneration (Lawesson, Oksanen 2002). In appropriate soils, natural *Q. robur* regeneration is common in *P. sylvestris* stands (Dobrowolska 2006; Goris et al. 2007). It is well known, that *Q. robur* is replaced by shade tolerant species, like *T. cordata* (Brumelis et al. 2011; Ikauniece et al. 2012).

Ecological succession after disturbance leads to a change in tree canopy composition determined by attributes of tree species (Noble, Slatyer 1980) and external drivers. Within the temperate zone, climate change, nitrogen deposition, density of large herbivores and forest management are drivers of vegetation change in forests (Bernhardt-Römermann et al. 2015). Long-term change of vegetation can be investigated by resurvey of plots (Verheyen et al. 2016), but availability of such plots can be limited. Historically, traditional forms of management in temperate forest maintained a mosaic of open structures (Bobiec et al. 2011), which has been converted to tall forest and loss of the species associated with this habitat. Therefore, human intervention has often been used to protect these conservation values (Götmark 2013).

Many temperate broad-leaved forest habitats are protected in the European Union. These include the habitats Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli (code 9160), Fennoscandian hemiboreal natural old broad-leaved deciduous forests (*Quercus, Tilia, Acer, Fraxinus* or *Ulmus*) rich in epiphytes (code 9020), Alluvial forests with *Alnus glutinosa* and *F. excelsior* (Alno-Padion, Alnion incanae, Salicion albae) (code 91E0), and Riparian mixed forests of *Q. robur, U. laevis* and *Ulmus minor, F. excelsior* or *Fraxinus angustifolia* along the great rivers (Ulmenion minoris) code 91F0 (http://eunis.eea.europa.eu/habitats.jsp). Generally, the protected broad-leaved forest habitat type in Europe have unfavourable status in danger of regionally disappearing or requiring change in policy of management. WIhin the period between 2006 and 2013, 64 million Euro was directed on restoration and conservation of forest habitat in EU LIFE projects, of which the majority (64%) of projects focused on temperate broadleaved forest (Bollen, Velghe 2015).

Efforts are being made to develop management guidelines for protected EU forests habitats, for example, in the LIFE+ funded project "National Conservation and Management Programme for Natura 2000 Sites in Latvia" implemented by the Nature Conservation Agency of Latvia (Ikauniece 2017). However, these guidelines can only provide a tool box of possible measures (Ikauniece 2017), and choice of the the most efficient method of intervention is based on limited experience of monitored trials. Knowledge of the past changes in canopy composition of broad-leaved woodland can be obtained from the existing tree age and size structure in stands. The aim of the current study was to determine the tree age structure in the canopy and size structure in the shrub layer of broad-leaved tree stands to determine past changes and to predict future trends in tree species composition and the conservation value. It was hypothesized that conservation value of broad-leaved stands was decreasing due to replacement of *Q. robur* by *P. abies*.

Materials and methods

Site description

Latvia is located in the transition zone between the continental and maritime climatic zones (Draveniece 2007). Mean annual temperature is 5.8 °C (Lizuma et al. 2007); mean annual precipitation is 703 mm with most falling in the warm period (Briede, Lizuma 2007). Climate continentality increases within Latvia to the East, and thus also raises effect of cold winters and summer drought as limiting factors for growth of broad-leaved tree species like *Q. robur* (Matisons et al. 2012).

Field sampling was conducted in 2015 to 2016 (26 plots) and we included data (24 plots) from another study (Ikauniece et al. 2013) that employed the same methods, but

Fig. 1. Location of studied plots in broad-leaved forest stands.

which was focused on understory herbaceous communities of oak stands. Forest stands were randomly selected from the Forest Register of Latvia (State Forest Service) from as much as possible all regions of Latvia based on the following criteria: broad-leaved tree species contributing at least 70% of total stand composition by wood volume, stand area > 1 ha, age > 60 years. However, the selected stands also included two coniferous stands with abundant *Q. robur* in the subcanopy and shrub layer, but where wood volume of broad-leaved tree species was < 70% of the total.

Size of selected stands was 1.4 to 34.9 ha. Location of the selected 50 stands is shown in Fig. 1. Plots with size 20 × 50 m were established within stands randomly but in sites without any human disturbances like forest roads.

In the plots, diameter at breast height (DBH) was measured for all trees with DBH >10 cm and cores were removed from all of these trees. All other stems were counted by species in height classes ≤ 1 m, 1.1 to 5 m, 5 to 10m.

Laboratory analysis and statistics

Obtained tree cores were glued in grooved planks, sanded, and then tree rings were counted under a Leica microscope or on scanned images using LignoVision 1.37 (Rinntech). Number of stems in 40-year age classes was determined for each tree species.

Cluster analysis (Sorensen distance measure, weighted mean linkage) was conducted on a matrix of tree number per age class of species. Optimal group size in the cluster analysis was determined by raising number of groups while maintaining significant differences (multiple response permutation procedure) between groups and minimal number of groups with one outlier plot. As tests of significance could not be conducted on groups with only one plot, these outliers were removed sequentially when increasing group number. The procedure was stopped when lack of significance arose between at least one pair of groups. Indicator species analysis was conducted to characterize groups by tree species basal area, and tree species age and shrub height classes. The analyses were conducted using PCORD 5.0.

Negative binomial generalized linear models as implemented in R 3.4.2. (R Core Team 2017) library MASS (Venables, Ripley 2002) were used to analyse influence of cluster groups on the density of tree species identified as indicator species. ANOVA was used to analyse influence of cluster groups on the basal area of each species. Multiple comparisons (Tukey contrasts, adjusted *p*-values) as implemented in library multcomp (Hothorn et al. 2008) were used to make pairwise comparisons of clusters after GLM or ANOVA analysis

Results

Cluster analysis

Cluster analysis resulted in 10 groups that differed in canopy composition and age structure (Fig. 2). The two groups with only one plot each represented stand types that were not common in Latvia. Of the randomly selected stands that were dominated by *F. excelsior*, most were not sampled due to extensive dieback. The other one-plot group was a young *Q. robur* stand, which had evidently developed on abandoned farmland (suggested by a plough layer in the soil). The other groups contained differing proportions of broadleaved tree species, black alder [*Alnus glutinosa* (L.) Gaertn.], *P. abies* and *P. sylvestris*. Four groups were distinguished by age of *Q. robur*.

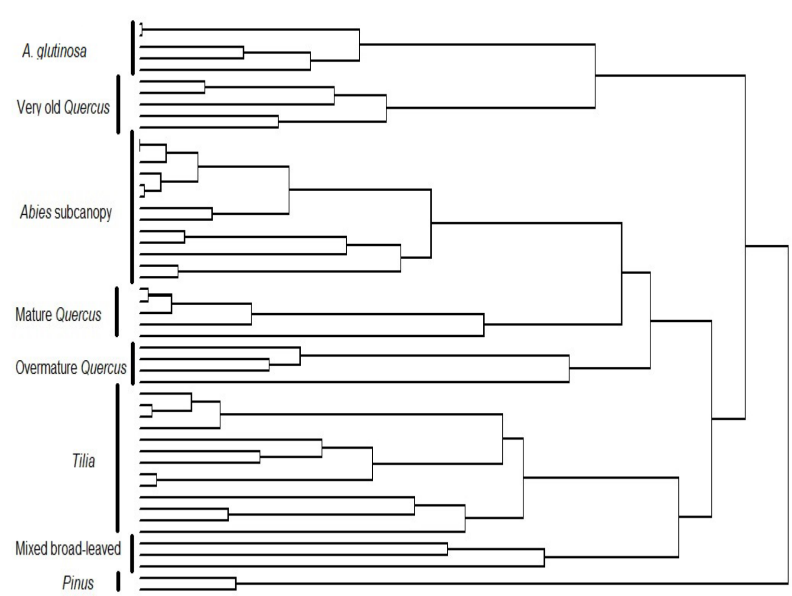

Fig. 2. Cluster analysis of broadleaved forest stands based on tree species composition in age classes.

Table 1. Mean basal area ha-1 by tree species in groups of broad-leaved tree stands (letters show similar groups according to Tukey post-hoc test)

	Undermature *Q. robur*	Mature *Q. robur*	Overmature *Q. robur*	Very old *Q. robur*	*P. abies* subcanopy	Dieback *F. excelsior*	*T. cordata*	Mixed broad-leaved	*A. glutinosa*/ *F. excelsior*	*P. sylvestris*
P. abies	0.0	3.4a	5.9ab	3.9a	12.3b	0.0	3.8a	2.6a	1.5a	0.1
Q. robur	21.5	29.9bc	30.4bc	40.5c	24.9bc	19.0	6.6a	9.5ab	31.0bc	1.0ab
F. excelsior	0.0	3.7	0.0	1.7	0.0	15.4	2.2	0.5	4.0	0.0
T. cordata	0.0	0.5a	0.0a	1.0a	0.2a	0.0	17.1b	1.8a	0.2a	0.0a
A. platanoides	0.0	0.0	0.0	0.0	0.3	0.0	1.5	3.7	0.0	0.3
Ulmus sp.	0	0.0	0.0	0.7	0.0	0	0.6	2.4	0.8	0.0
A. glutinosa	0.0	0.0a	0.0a	0.0a	0.0a	0.0	0.2a	0.6a	4.6b	0.0a
Betula sp.	0.0	2.1	2.2	0.4	3.0	0.0	3.4	4.8	1.2	0.5
P. tremula	0.0	0.0	0.0	0.0	0.7	0.0	5.8	7.4	0.3	0.0
P. sylvestris	0.0	1.6a	1.9a	0.0a	0.7a	0.0	0.4a	0.0a	0.0a	29.2b

Basal area

Basal area of *Q. robur* was greater than 75% of the total basal area in five groups. Of these, spruce had about 7 to 15% of the total basal area in three groups (Table 1). Basal area was progressively larger in the undermature to mature, overmature and very old *Q. robur* groups, significantly higher in the very old *Q. robur* group. Other groups were distinguished by significantly higher basal area of *A. glutinosa, P. abies* or *F. excelsior, T. cordata* or *P. sylvestris*. The mixed broad-leaved stands had significantly higher basal area of silver birch (*Betula pendula* Roth), *P. tremula* and *A. platanoides*. One group with one stand had the largest basal area of *F. excelsior*.

Age structure

Three stand groups were identified in indicator species analysis as having significantly higher number of *Q. robur* in age classes 80 to 120, 121 to 160 or > 160 years in the mature, overmature and very old *Q. robur* groups, respectively (Table 2). One group with lesser number of *Q. robur* in all age classes had significantly higher amounts of *P. abies* with age 81 to 120 years. The age of the young *Q. robur* stand with age 81 to 120 years lacked other tree species. *Q. robur* with age 40 to > 200 years was common also in a group with significantly higher number of stems of *A. glutinosa*. Two stand groups contained mixtures of broad-leaved trees species, one with significantly higher amounts of *T. cordata* with age 40 to 120 years and the other with *A. platanoides* with age 40 to 80 years. The sole stand in the *F. excelsior* group contained low amounts of living ash and lacked other tree species. Number of *Q. robur* with age < 40 was significantly higher in the *P. sylvestris* stand group.

Sapling layer

P. abies occurred in all stand groups, with lower abundance in the taller height classes (Table 3). In the sapling layer, *Q. robur* was generally restricted to the < 1.0 m height class, except in pine stands, but had high abundance in the very old *Q. robur* and *F. excelsior* stands. In *P. sylvestris* stands, *Q. robur, Betula* sp. and *Acer* sp. generally had significantly higher abundance in all sapling layers. *F. excelsior* saplings were abundant in the < 1.0 m height class in all groups except the undermature and overmature *Q. robur* stands, and reached the 5.1 to 10.0 m layer in significantly higher number in the *A. glutinosa* and mature *Q. robur* stands. *T. cordata* had significantly higher sapling density in all height classes in the *T. cordata* group, and was abundant in < 1.0 m and 1.1 to 5.0 m classes in the *F. excelsior* and mixed broad-leaved stand groups. *A. platanoides* was common in all groups except the *A. glutinosa* stands, with highest abundance in the mixed broad-leaved stands. *Ulmus* sp. had highest abundance in the *T. cordata*, mixed broadleaved, and *A. glutinosa* stands in the < 1.0 m and 1.1 to 5.0 m layers. Grey alder [*Alnus incana* (L.) Moench] and *P. tremula* were fairly abundant in some of the groups, but only in the < 1.0 m layer.

Table 2. Mean density of tree stems >10.cm diameter at breast height (number 0.1 ha-1) by age class in groups of broad-leaved tree stands (letters show similar groups according to Tukey post-hoc test)

	Age (years)	Under-mature *Q. robur*	Mature *Q. robur*	Over-mature *Q. robur*	Very old *Q. robur*	*P. abies* sub-canopy	Dieback *F. excelsior*	*T. cordata*	Mixed broad-leaved	*A.glutinosa/ F. excelsior*	*P. sylvestris*
P. abies	< 41	0	0.4	2.5	0.2	2.5	0	0.2	0.0	0.2	0.5
	41–80	0	7.4b	2.5bc	0.6c	24.3a	0	3.8bc	1.7bc	2.0bc	0.0abc
	81–120	0	0.4	4.0	3.2	5.0	0	3.3	1.0	0.4	0.0
	121–160	0	0.2	1.5	0.6	0.0	0	0.9	0.3	0.0	0.0
Q. robur	< 41	1	0.0	0.0	0.0	0.2	0	0.0	0.0	0.0	3.0
	41–80	32	1.6	0.5	0.0	3.4	0	0.2	1.0	0.4	3.5
	81–120	0	20.8a	1.3b	0.2b	3.6ab	0	1.2b	3.7ab	0.2b	0.0ab
	121–160	0	0.2b	10.5a	0.2b	4.4ab	0	1.0b	0.7b	3.2ab	0.0ab
	> 160	0	0.0ab	2.0ab	13.4b	2.9ab	2	1.5a	1.0ab	6.4ab	0.0ab
F. excelsior	< 41	0	0.0	1.0	0.4	0.0	0	0.0	0.0	1.0	0.0
	41–80	0	2.4ab	0.0ab	2.0ab	0.2b	2	0.4b	0.7ab	8.8a	0.0
	80–120	0	1.0	0.0	0.2	0.2	5	1.4	0.0	1.0	0.0
	120–160	0	0.2	0.0	0.2	0.0	1	0.2	0.0	0.0	0.0
T. cordata	< 41	0	1.0	0.0	1.2	0.7b	0	2.8	0.3	0.2	0.0
	41–80	0	2.2b	0.0ab	1.4b	0.3b	0	18.2a	2.0ab	0.0ab	0.0ab
	81–120	0	0.0ab	0.0ab	0.0ab	0.0ab	0	8.0b	0.3ab	0.2a	0.0ab
	121–160	0	0.0	0.0	0.0	0.0	0	1.2	0.0	0.0	0.0
A.platanoides	< 41	0	0.0ab	0.0ab	0.0ab	0.0ab	0	0.2a	0.0ab	0.0ab	2.0b
	41–80	0	0.2b	0.0ab	0.0ab	0.5b	0	1.1b	8.0a	0.0ab	0.0ab
A. glutinosa	< 41	0	0.0	0.0	0.0	0.0ab	0	0.0	0.0	0.8	0.0
	41–80	0	0.2bb	0.0ab	0.0ab	0.0ab	0	0.5ab	0.0ab	13.8a	0.0ab
Betula sp.	<41	0	0.0	0.0	0.0	0.5	0	0.1	0.0	1.0	1.0
P. tremula	81–120	0	0.0ab	0.0ab	0.2ab	0.3a	0	3.8b	3.0ab	0.2ab	0.0ab
P. sylvestris	41–80	0	0.0ab	0.0ab	0.0ab	0.0ab	0	0.0ab	0.0ab	0.2a	6.5b
	81–120	0	0.8	0.3	0.0	0.3	0	0.0	0.0	0.0	18.5

Table 3. Mean density of samplings <10 cm diameter at breaast height (number 0.1 ha-1) by height class in groups of broad-leaved tree stands (letters show similar groups according to Tukey post-hoc test)

	Height (m)	Under-mature *Q. robur*	Mature *Q. robur*	Over-mature *Q. robur*	Very old *Q. robur*	*P. abies* sub-canopy	Dieback *F. excelsior*	*T. cordata*	Mixed broad-leaved	*A.glutinosa/ F. excelsior*	*P. sylvestris*
P. abies	< 1	35	1	12	9	14	2	10	1	3	0
	1.1–5.0	6	26	15	6	18	5	30	4	2	1
	5.1–10	2	2	3	0	5	0	4	2	1	0
Q. robur	< 1	85	138	10	478	32	445	8	3	29	36
	1.1–5.0	0	0ab	0ab	0ab	0a	0	0ab	0ab	0ab	30b
	5.1–10	0	0	1	0	0	0	0	0	0	6
F. excelsior	< 1	0	711	3	402	36	195	112	500	714	0
	1.1–5.0	0	16	0	3	2	0	6	5	25	0
	5.1–10	0	5ac	0ab	1bc	0b	0	1b	0ab	17a	0ab
T. cordata	< 1	0	4b	15ab	6b	10b	55	131a	30ab	1b	0ab
	1.1–5.0	0	6ab	9ab	2b	3ab	5	68a	23ab	0ab	0ab
	5.1–10	0	2ab	1b	1b	0b	0	14a	1ab	0ab	0ab
A.platanoides	< 1	41	49	3	8	516	65	337	566	0	20
	1.1–5.0	2	2	0	4	5	0	14	9	0	1
	5.1–10	1	1	0	0	1	0	3	6	0	0
Ulmus	< 1	0	1	0	9	10	0	60	84	63	0
	1.1–5.0	0	1	0	3	2	0	14	16	3	0
Betula sp.	< 1	0	0	0	0	4	0	0	1	0	11
	1.1–5.0	0	0	0	0	1	0	0	3	0	27
	5.1–10	0	0ab	0ab	0ab	0b	0	0b	0ab	2ab	9a
A.incana	< 1	0	0	42	10	8	0	0	11	1	0
P. tremula	< 1	1	2	49	10	17	0	24	31	35	2

Discussion

The broad-leaved tree woodland in Latvia that is classified as protected habitat in the European Union is identified using criteria of tree canopy composition, understorey vegetation, epiphytes and structural indicators (Auniņš 2013). In the current study by focusing on canopy composition and age we identified nine groups of broad-leaved stands and one coniferous group with large amounts of broad-leaved tree species in the understorey tree layers. The effect of canopy composition on understorey vegetation and soil forming processes is well known (Hagen-Thorn et al. 2004; van Oijen et al. 2005). The classification obtained in this study was based only on determination of different successional stages of canopy development, which might be used to guide management for conservation of biological diversity.

Establishment of *P. abies* and its encroachment in the canopy is expected to cause changes like higher rate of accumulation of organic matter (Bonifacio et al. 2008) and lower pH, which can retard colonization and growth of nemoral species (Brunet et al. 1997; Brunet et al. 2011). Picea abies was regenerating in the understorey in most of the broad-leaved tree species stand groups and had reached the 80–120 year age class. This indicates continuous successful establishment of this shade-tolerant species in the stands. Conversion of *Q. robur* to *P. abies* stands has been previously documented in Latvia (Tērauds et al. 2011). Conservation of the nemoral values of the stands should thus focus on the cutting of this tree species when present.

Tilia cordata was common in the broad-leaved tree stand groups in all tree layers, and in one group was the dominant tree species. Succession of tree species to increased proportion of *T. cordata* has been previously described in the boreo-nemoral forest zone (Brumelis et al. 2011) and as a tolerant species can be the dominant species on richer soils (Pigott 1991). The leaf litter of *T. cordata* is basic, which promotes cycling of elements (van Oijen et al. 2005) and a nemoral flora and associated epiphyte community is typical of these stands (Mezaka et al. 2012; Auniņš 2013). The results suggest that a suitable conservation management method in broad-leaved stands would be to promote growth of the fairly shade tolerant *T. cordata* by reducing competition by *P. abies*.

Quercus robur was the dominant species by basal area in seven of the ten broad-leaved species tree groups, and common in the <1.0 m height class of samplings. However, there was no evidence of establishment in higher height classes of the tree layers of the broad-leaved tree stand groups, as observed previously (Faliński 1988; Brumelis et al. 2011). Nevertheless, as shown in this study and previously (Götmark et al. 2005; Goris et al. 2007), *Q. robur* can successfully regenerate in coniferous stands provided suitable light conditions, as in the studied *P. sylvestris* stand group. This suggests a need for research on growth of *Q. robur* on dry site types in the boreo-nemoral forest zone, as in the *P. sylvestris* stands, to determine potential future outcome. Also, it is possible that creation of gaps with suitable size might promote establishment of *Q. robur* in stands on richer soils, provided thinning is conducted and enclosures are established to prevent browsing by ungulates (Leonardsson et al. 2015). However, the main aim of conservation of these stands should be the reduction of their spatial fragmentation by planting new stands and conserving natural regeneration of *Q. robur* in clearcuts.

There was only one *F. excelsior* stand investigated, as most of the randomly selected had degenerated due to disease caused by *Hymenosccyphus fraxinus*, as throughout Europe (Pautasso et al. 2013). Regeneration of *F. excelsior* is still occurring in stands suffering dieback in Latvia (Pušpure et al. 2017), but stand conversion to other broad-leaved species might be warranted, particularly when present in the canopy and other tree layers.

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