Research Article

Initial impact of clear-cut logging on dynamics of understory vascular plants and pollinators in Scots pine-dominated forests in Lithuania

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Abstract: The development of understory plants and attendant changes of pollinators immediately after clear-cut logging were studied in boreal Scots pine forests. Experiments were carried out in *Vacciniosa* and *Vaccinio-myrtillosa* forest types. Considerable decline of the dwarf shrub layer confirmed the negative reaction of this dominated understory life form; however, the frequency dynamics of different vascular plants demonstrated species-specific response to changing environmental conditions. Because of rapid changes of light as well as damage of rhizomes by soil disturbances, the values of mean cover and frequency of the studied Ericaceae species decreased. We detected the most sensitive understory species to be *Lycopodium annotinum*, *Arctostaphylos uva-ursi*, and *Goodyera repens*; consequently, their preservation is possible only under sustainable forest resources exploitation. On the other hand, arrival of new light-demanding species caused increased pollinator visitation to focal ericaceous shrubs.

Key words: Ericaceae, clear-cutting, understory vegetation

1. Introduction
Present-day activities in forest management involve different aspects of biodiversity such as exploitation of non-wood forest products and the monitoring of rare and threatened plant and insect species. Maintenance of managed forest resources influences the ecosystem on different levels: genes, individual organisms, species, and populations. Therefore, the complex forest ecosystem requires the implementation of the sustainable use of forest resources. Accordingly, information on the structural components of forests and their responses to various management activities is necessary (Spiecker, 2003).

The handling of timber and clearing-cutting cause the destruction of understory plants and the alteration of the forest floor structures. Clear-cuts followed by intensive soil preparation, scarification, and planting substantially influence the biodiversity because these works disturb natural forest dynamics (Bergstedt et al., 2008; Paillet et al., 2010). Thereby, human activities not only strongly affect the vertical structure of different forest habitats but also change the composition and the distribution of trees, shrubs, and herb species and the amount of litter

in forest ecosystems. Intensive clear-cut logging with harvesting of forest woody debris and soil preparation for new tree planting affect the ground flora strongly. Vanha-Majamaa et al. (2017) reported that resilience was greater for vascular plants, especially for herbs, than for mosses in Norway spruce forests. Other studies revealed the species-specific responses to tree extraction and demonstrated considerable differences within plant functional groups, e.g., shrubs and herbs (Tonteri et al., 2016). Forest management can accelerate the loss of native species through habitat destruction or alteration and the introduction of invasive species (Gilliam, 2007). Many studies demonstrated that undisturbed forests are resistant to invasions, even being surrounded by damaged forests as potential source of different invasive species (Luken, 2003; McCarthy, 2003).

Scots pine (*Pinus sylvestris* L.) is common and economically one of the most important tree species in the boreal forests of Europe. The prevailing Scots pine forests are widespread in the boreal part of northern hemisphere. Scots pine occupies about 716,000 ha in Lithuanian forests, which translates to 34.8% of the total forest area

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(Ministry of the Environment, 2016). These stands grow on poor acid soils and their ground vegetation is characteristic by abundant layers of mosses, lichens, and ericaceous shrubs. Such species composition is determined by natural factors (Ellenberg et al., 1991). The most abundant understory vascular plant species are *Vaccinium myrtillus* L., *V. vitis-idaea* L., and *Calluna vulgaris* L. (Hull), which also represent natural resources of nontimber forest products (Clason et al., 2008; Heinrichs and Schmidt, 2009; Hekkala et al., 2014). *V. myrtillus* and *V. vitis-idaea* are not only valuable berry plants in boreal pine-dominated forests but also important functional species for forest pollinators (Rodriguez and Kouki, 2015). *C. vulgaris* also offers pollen and nectar at the end of summer and supports large numbers of insects (Descamps et al., 2015). Generally, the understory vegetation in temperate forests contains about 90% of all forest species, significantly contributing to cycling rates of soil nutrients (Gilliam, 2007).

Estimation of initial changes of forest species to the damages is important for the prediction of their resistance and implementation of recovering of forest ecosystem. As Vanha-Majamaa et al. (2017) emphasized, the resistance of understory plant species can be estimated immediately after cutting, whereas a longer time period is needed to study their resilience. Our study aimed at assessing the short-term initial response of the understory vascular plants and pollinators in Scots pine forests after clearcut logging. More specifically, we focused on changes in vascular species diversity and distribution, responses of endangered plant species to clear-cuts, and activity of pollinators of Ericaceae shrubs in mature and clear-cut forest areas.

2. Materials and methods

2.1. Study sites
We chose Scots pine-dominated forests types of *Vacciniosa* (PV) and *Vaccinio-myrtillosa* (PVM). The study plots were situated in SE Lithuania (Figure 1). Nine PV study plots were selected from 54°11′62″N to 54°25′61″N and 24°33′13″E to 24°49′16″E, whereas the same number of PVM study plots were chosen from 54°24′37″N to 54°23′49″N and 25°00′03″E to 24°57′22″E. The forest type was determined in accordance with prevailing tree species, understory vegetation, forest soil pH, and humus fraction (Karazija, 2003; Navasaitis et al., 2003). Mature forests of PV were characterized by prevailing tree species *P. sylvestris* and sporadically growing *Betula pendula* Roth with the same species in underwood. The diagnostic understory vascular plant species were *V. vitis-idaea*, *Festuca ovina* L., *C. vulgaris*, and mosses *Dicranum polysetum* Sw. and *Pleurozium schreberi* (Willd. ex Brid.) Mitt. Mature PVM forests sites were characterized by dominated tree species *P. sylvestris* and sporadically growing *Picea abies* (L.) H.Karst and *B. pendula*. *P. abies* was the dominated tree species

in the underwood, whereas *P. sylvestris* was rather sparse in this layer. The diagnostic understory species were *V. myrtillus*, *Melampyrum pratense* L., *V. vitis-idaea*, *Luzula pilosa* (L.) Willd., *Trientalis europaea* L., and moss species *Ptilium crista-castrensis* (Hedw.) De Not. The total cover of vascular plants varied from 10%–16% (mature stand of PV forest type) to 14%–42% (mature stand of PVM forest type). Nevertheless, mosses dominated in both forest types covering, on average, 70% to 85%. pH_{KCl} was determined in 1 mol/L suspension (ISO 10390:2005) and humus fraction was determined according to ISO 10694:1995. PV forests stands were characterized by very infertile acid soil with 1.5%–2% of the humus fraction, while the humus fraction in PVM reached ca. 3%. The soil pH_{KCl} varied from 4.2 to 4.4 in both PV and PVM forest stands. The depth of crude forest floor was, on average, 2–4 cm.

The forest sites were selected in mature stands of average age 115–130 years and measured 2.4–3.4 ha. The stand volume range varied from 330 to 335 m^3 per hectare and the average diameter of trees reached from 31 to 37 cm. The study plots were situated in lowland with an average yearly temperature of 6.8 °C and average annual precipitation of 700 mm. According to the data from the nearest weather station, the mean temperature is 17.9 °C in July and –3.7 °C in January. Part of each study plot was cleared and tree stems, where roots and big branches were removed in 2015. Our experiment was therefore implemented on control intact (mature) forest plots (Figure 2 a), which were compared with samples obtained from cleared subplots (Figure 2b). Data sampling was conducted twice: 1 year after clear-cutting (in 2016) and then in 2017 (2 years after clear-cutting).

2.2. Evaluation of understory vegetation data
For the average vegetation cover, the frequency of understory vascular plant species was estimated in 1 m^2 subplots (the frame of 1 dm^2 square mesh was used with 30 replicates). Average cover (%) of each species was assessed visually. Frequency of each species was determined as follows: number of plots in which the particular species was detected divided by total number of subplots (Ehlers et al., 2003). The indicator values of the most abundant plant species (average cover ≥1%) were determined by multiplying the relative abundance and relative frequency (Dufrêne and Legendre, 1997). We estimated changes of vascular plant abundance according to ecological indicator values of different species (Ellenberg et al., 1991). To determine the functional effect of clear-cuts on vascular plant species, different life forms were indicated as follows: dwarf shrubs, annual herbs, and perennial herbs.

2.3. Observations of pollinators
For pollinator observations we chose the ericaceous species because their average cover and frequency were sufficiently high in the sites of investigations. Field

Figure 1. Mature forest (a) and clear-cut (b) study plots.
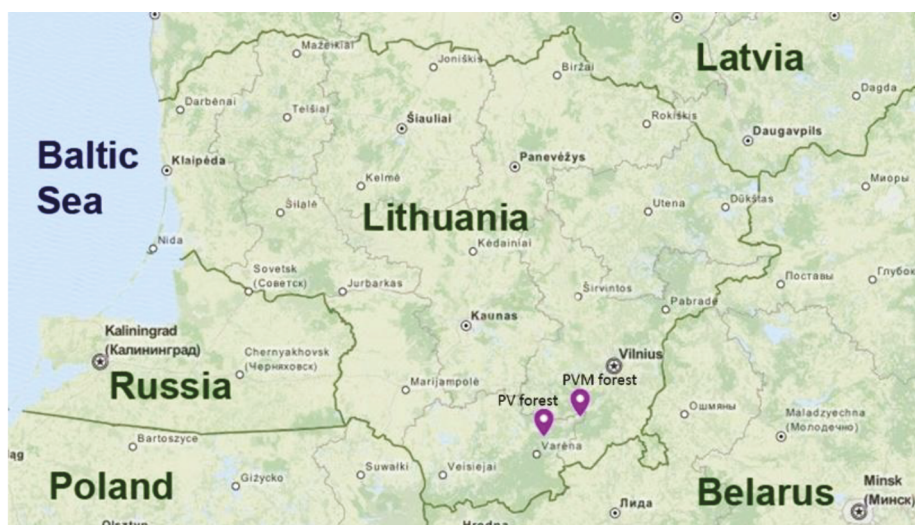

Figure 2. Locations of *Vacciniosa* (PV) and *Vaccinio-Myrtillosa* study plots in SE Lithuania.

observations of floral visitors were completed in 2017 during peak flowering period of our study plants. For recording insect activities we used digital video cameras (HDR-PJ810E, SONY), which is a standard procedure in similar studies (see, e.g., Lortie et al., 2011; Niemirski and Zych, 2011; Zych et al., 2013, 2014; Daubaras et al., 2017). For each site we completed at least 12 rounds of video recordings on both clear-cut and mature stands (control). Each recording lasted about 15 min on a randomly chosen patch of flowering plants (5–15 flowers).

Each study day recordings commenced at 1000 hours and ended at 1600 hours at latest. No more than eight were completed in a single day, which means that for a single site observations lasted at least two full days or longer since during inclement weather (strong winds or rain),

observations were halted and recommenced on subsequent days. Recordings were then analyzed for the number of visits by particular insects. We assigned floral visitors to broad functional groups: honeybees, bumblebees, solitary bees, wasps, ants, muscid flies, syrphid flies, butterflies, and beetles. The remaining insects, if present, were treated as "other".

2.4. Statistical analysis

Statistical data mining was performed using MATLAB v9.1 (R2016b) software. Data analysis included hypothesis testing to determine the significance of changes in frequency and average cover of vascular plant species after clear-cut logging. Hypothesis testing was carried out applying two-tailed paired-sample t-tests and two-tailed two-sample t-tests at a significance level of $\alpha = 0.05$. The

paired-sample t-test was applied for testing the hypothesis about the mature forest stand being invariant during these 2 years, while the two-sample t-test was performed for comparing the mature forest stand as a control and clear-cut area measurement results.

In the case where the H_0 hypothesis about the means of the tested variables being equal was rejected at the chosen significance level, the two-tailed hypothesis result was converted to a one-tailed hypothesis to confirm either incremental or decremental statistically significant change. After hypothesis testing a cumulative similarity measure (Euclidean distance) calculation was performed to obtain information about overall "closeness" tendencies of the investigated areas during 2 years.

Data on dynamics of different plant life forms and insect visits were tested using one-way ANOVA. Duncan's multiple range test was used to compare mean values based on ANOVA results.

3. Results

3.1. Response of life forms of understory vascular plants to clear-cut logging

The dwarf shrubs layer was the dominant vascular plant guild of the studied forest types. It was most developed in mature PVM forest areas and occupied 41%, on average (Figure 3). Substantial decline of shrub cover was detected immediately after cuts in all plots in 2016. Dwarf shrub cover started to increase slightly in the PV forest type 2 years after clear-cut logging (Figure 3). Perennial herbs were rare in mature stands of PV and PVM forest types with an average cover from 1.4% to 1.9%. Moderate changes in mean cover of perennial herbs were observed in both forest types during 2 years after clear-cut logging. Annual herbs started to appear in PVM clear-cut areas in 2017. This vegetation guild increased substantially after clear-cut logging of PV forest stands (Figure 3). Total cover of understory vascular plants varied from 13.1% to 42.6% in mature stands and decreased from 7.9% to 12.6% depending on forest type in the cut areas 2 years later.

3.2. Dynamics of particular species

The response of vascular plants to clear-cut logging was species-dependent. Figures 4a, 4b, 5a, and 5b show changes in average cover and frequency of different species in the investigated areas after clear-cuts in 2016 and 2017.

The negative impact of clear-cuts was stronger for *V. myrtillus* when compared to *C. vulgaris* and *V. vitis-idaea*. Increased light intensity because of tree removal and soil cover destruction during soil preparation negatively influenced populations of *V. myrtillus*, resulting in significant decrease in frequency and mean cover in clear-cut areas of PV and PM forests (Figures 4a, 4b, 5a, and 5b). Mean cover and frequency of *C. vulgaris* increased due to the arrival of new seedlings in all study plots 2 years after

clear-cut logging. *V. vitis-idaea* showed moderate response in cut areas of both forest types. In fact, we observed progressive changes of average cover and frequency of this species 2 years after clear-cuttings. *V. vitis-idaea* was distinguished by significant indicator value of ≥10 in mature stands and the increasing of this value was observed in clear-cut sites of PVM (Table). *V. myrtillus* was a prevailing ericaceous dwarf shrub in mature stands of PVM; however, clear-cutting affected the indicator value of this species.

The results for mature forest stands of PV forest type showed that new vascular plant species (*Spergula arvensis* L., *Calamagrostis epigeios* (L.) Roth, *Rumex acetosella* L., *Corynephorus canescens* (L.) Beauv., *Senecio vulgaris* L., *Hieracium* sp., and *Veronica officinalis* L.) appeared in 2016, and the number of newcomers increased in 2017 (Figures 4a and 4b). The rapid expansion was characteristic for *Rumex acetosella*. The analysis also showed statistically significant results for *Epilobium angustifolium* L. and *S. vulgaris* in 2017. These species were characterized as light-demanding or preferring well-lit places with light indicator values of 6–8 (Table). Generally, all forest-related vascular plants decreased in coverage and frequency or disappeared in clear-cut plots of PVM forest type (Figures 5a and 5b). For example, *Convallaria majalis* L., *Trientalis europaea* L., *Luzula pillosa* (L.) Willd., and *Arctostaphylos uva-ursi* (L.) Spreng. had already disappeared 1 year after clear-cut logging. Endangered species restricted to mature forest stands, namely clubmoss *L. annotinum* L. and *G. repens* (L.) R.Br., vanished also. However, these species were rare in mature stands. On the other hand, logging resulted in three new species, *E. angustifolium*, *S. vulgaris*, and *Carex caryophyllea* Latour., to be listed in 2017 (Figures 5a and 5b).

Statistical analysis also involved calculation of Euclidean distance, representing a cumulative similarity measure, which allowed comparing the mature stand and clear-cut areas (Figure 6). The data clearly showed that, despite the forest type, the dissimilarity measure based on the Euclidean distance between control and clear-cut sites increases over time.

3.3. Pollinators

Overall, we recorded 103 insect visits to our studied plants. The most diverse floral visitor assemblage was that for *C. vulgaris*, and its flowers were visited by ants, bumblebees, solitary bees, honeybees, butterflies, syrphids, muscid flies, and other insects. Flowers of *V. vitis-idaea* were visited by ants, butterflies, solitary bees, and honeybees and flowers of *V. myrtillus* only by ants. Average visit frequency was generally low for *Vaccinium* species, at 0.5 ± 1.2 and 0.4 ± 0.7 visits/15 min, respectively, for *V. vitis-idaea* and *V. myrtillus*, and moderate for *C. vulgaris* (4.1 ± 4.3 visits/15
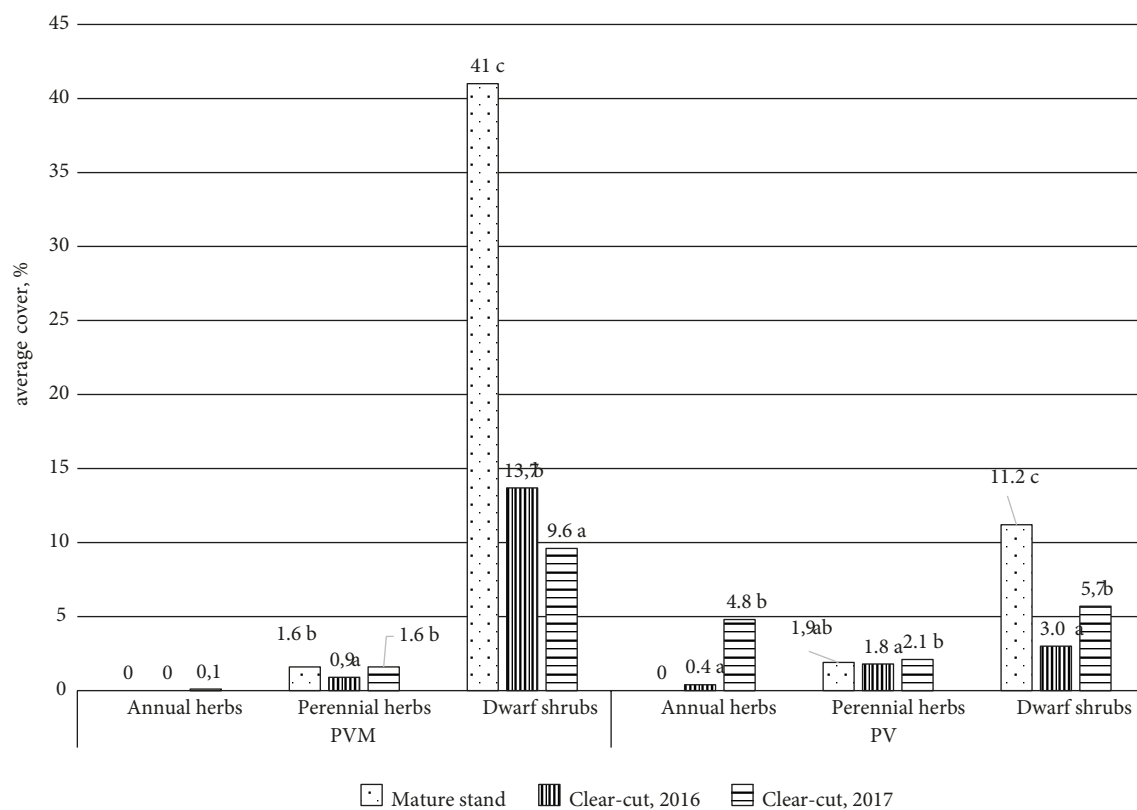
Figure 3. Mean cover of different life forms of vascular plants in response to clear-cut logging in *Vacciniosa* (PV) and *Vaccinio-myrtillosa* (PVM) forests. Different letters indicate significant differences among the particular life form (Duncan's multiple range test, α = 0.05).

min). Because our dataset contained many zeros, we decided to pool the data across sites in order to detect the impact of logging on particular plant species (Figure 7).

For all three studied species plants tended to be visited more frequently in clear-cut sites; this difference, however, was statistically significant only for *V. myrtillus* and *C. vulgaris*.

4. Discussion
Light and moisture requirements of vascular plants may substantially determine their adaptability (Heinrichs and Schmidt, 2009; Tonteri et al., 2016). However, the responses are often species-specific and may differ depending on the forest type. For example, *V. vitis-idaea* and *C. vulgaris*, shrubs from the family Ericaceae, demonstrated particular resistance in PVM forests (Figures 5a and 5b). Similar consistent tendencies were found in previous studies comparing effect of cuts on understory plants. Tree overstory removal causes early successional changes of understory vegetation guilds and species composition because of improved light conditions and soil fertility variation (Vanha-Majamaa et al., 2017). In

our study, new herb species that appeared in clear-cut sites were characterized by high demand for light and preferred more fertile soils (Table). Rapid spread was determined for anemochorous species *R. acetosella*, *E. angustifolium*, and *S. vulgaris* (Appendix). We observed significant decrease in cover and weak recovery for *V. myrtillus*, especially when compared to *V. vitis-idaea*, which is in accordance with earlier studies (Atlegrim and Sjöberg, 1996; Tonteri et al., 2016). Stump harvesting in particular seems most harmful for the Ericaceae species *V. vitis-idaea* and *V. myrtillus* because it increases the area of disturbed soil surface compared to conventional harvesting (Andersson et al., 2017). Interestingly, Vanha-Majamaa et al. (2017) reported that *V. myrtillus* did not recover in boreal Norway spruce forests 10 years after cuts. However, other authors (Atlegrim and Sjöberg, 1996; Nybakken et al., 2013) predicated that *Vaccinium* shrubs may withstand physical damages because of nutrient reserves in underground parts and rapid spread by rhizomes. We observed a slight increase of *V. vitis-idaea* abundance even 2 years after clear-cutting, and in similar studies the faster spread of *V. vitis-idaea* compared to *V. myrtillus* was reported 3–4 years
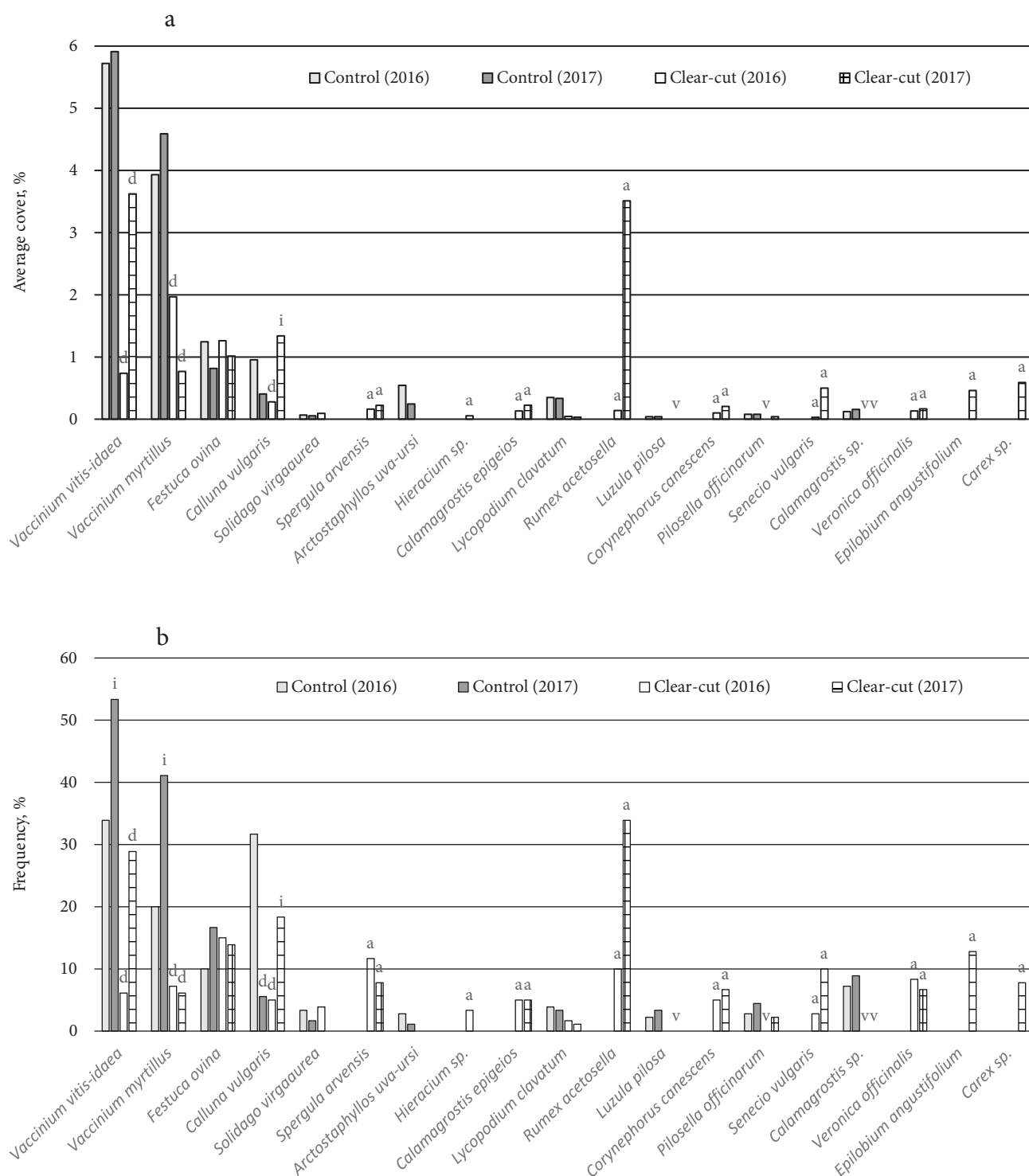
Figure 4. Average cover (a) and frequency (b) of observed understory vascular plant species in PV forests in 2016 and 2017. Statistically significant changes (i: increased, d: decreased, a: appeared, v: disappeared) of the first comparand with regard to second comparand are presented as follows: mature stand (2017) vs. mature stand (2016), clear-cut (2016) vs. mature stand (2016), and clear-cut (2017) vs. mature stand (2017). Significance level of all noted changes is α = 0.05.
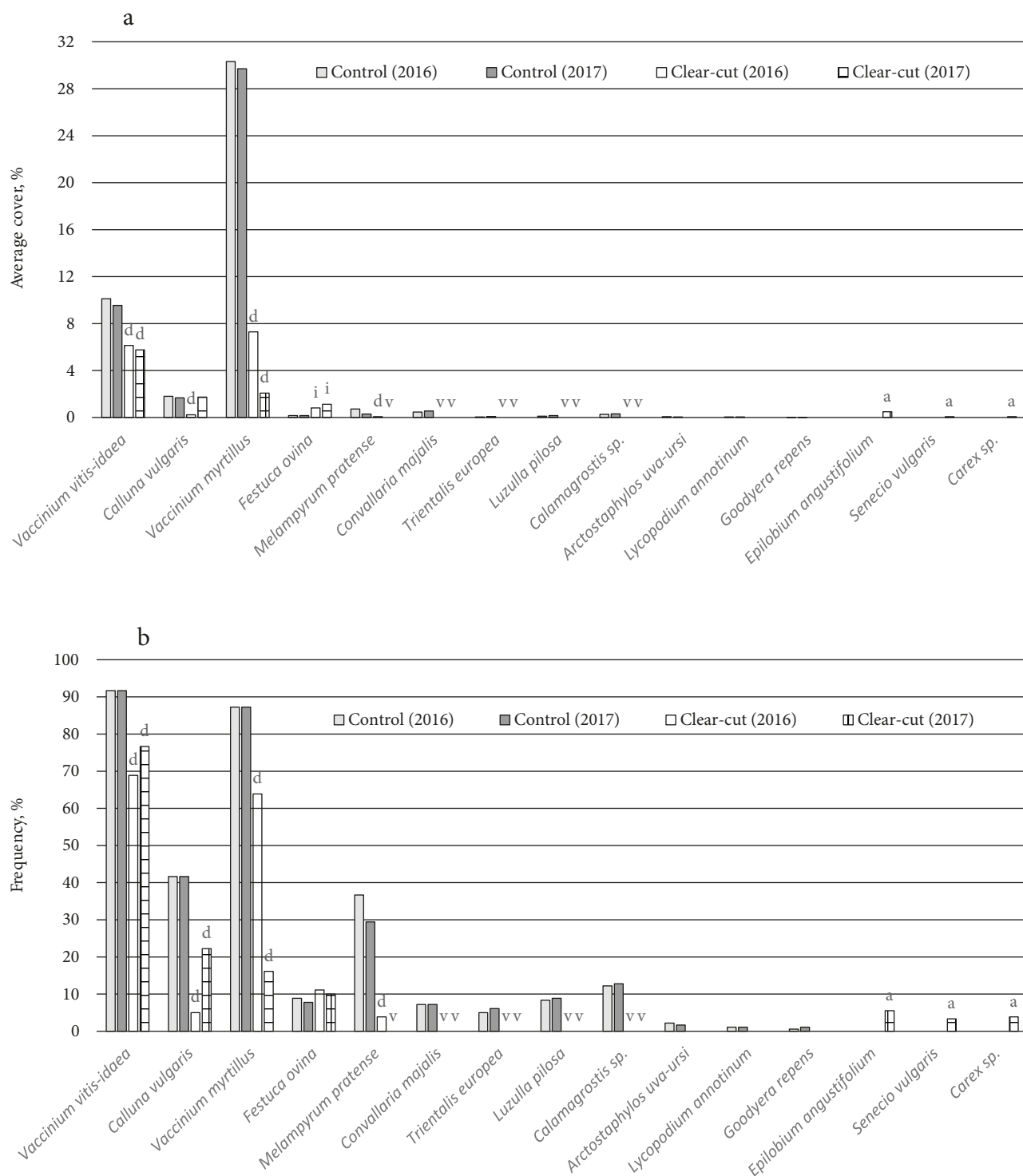
a

b

Figure 5. Average cover (a) and frequency (b) of observed understory vascular plant species in PVM forests in 2016 and 2017. Statistically significant changes (i: increased, d: decreased, a: appeared, v: disappeared) of the first comparand with regard to second comparand are presented as follows: mature stand (2017) vs. mature stand (2016), clear-cut (2016) vs. mature stand (2016), and clear-cut (2017) vs. mature stand (2017). Significance level of all noted changes is α = 0.05.

Table. Indicatory values of understory vascular plant species in mature forest and clear-cut sites.

Taxa names	Species indicator values						Ecological indicator values*	
	Vaccinio-myrtillosa			*Vacciniosa*			L	N
	Control	Clear-cut, 2016	Clear-cut, 2017	Control	Clear-cut, 2016	Clear-cut 2017		
Vaccinium myrtillus	60.9	30.0	4.1	6.5	3.3	+	5	3
V. vitis-idaea	21.5	32.6	39.5	16.3	1.2	8.3	5	1
Calluna vulgaris	1.7	+	3.49	2.4	+	2.6	8	1
Festuca ovina	+	+	1.33	1.8	+	1.7	7	1
Melampyrum pratense	+	+					x	2
Conavallaria majalis	+						5	4
Luzula pillosa	+			+			2	4
Calamagrostis epigeios	+				+	+	7	6
Arctostaphylos uva-ursi	+			+			6	2
Lycopodium clavatum				+	+	+	8	2
L. annotinum	+						3	3
Corynephorus canescens					+	+	8	2
Pilosella officinarum				+		+	7	2
Spergula arvensis					+	+	7	5
Trientalis europaea	+						5	2
Goodyera repens	+						5	2
Senecio vulgaris			+		+	+	7	8
Solidago virgaurea				+	+		5	4
E. angustifolium			+			+	8	6
Veronica officinalis					+	+	6	4
Rumex acetosella					+	9.9	8	2
Carex caryophyllea			+			+	8	2

+: Average cover ≤1%.
*L: Light, N: soil fertility, x: broad amplitude or unknown (Ellenberg et al., 1991).
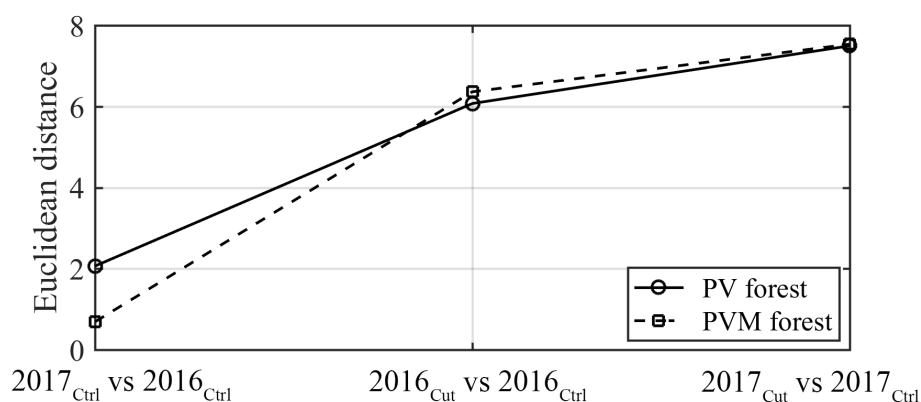
Figure 6. Euclidean distance as an overall similarity ("closeness") measure between two particular areas, described by herbs and shrubs average cover and frequency.
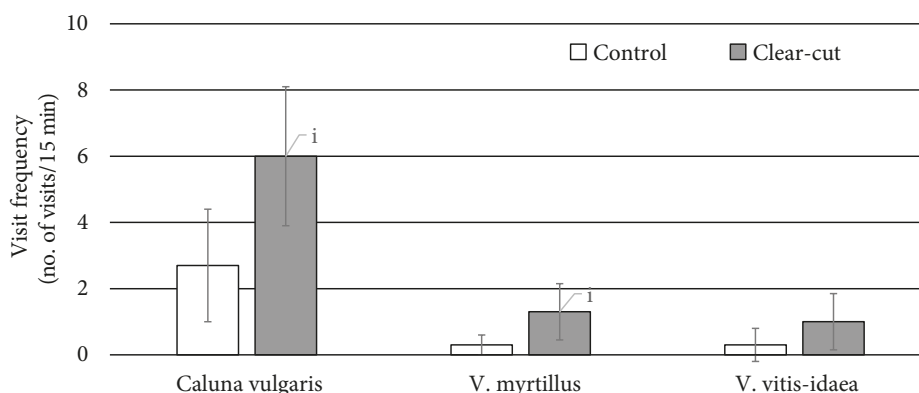
Figure 7. Frequency of insect visits (no. of visits/15 min) to flowers of three ericaceous plants, *C. vulgaris* ($F_{(1.38)}$ = 6.1765, P = 0.017), *V. myrtillus* ($F_{(1.22)}$ = 7.0798, P = 0.014), and *V. vitis-idaea* ($F_{(1.37)}$ = 1.7775, P = 0.19), in mature forest stands (control) and logged sites (clear-cut). Data were pooled over all study sites and means were compared using one-way ANOVA. Error bars represent 0.95 confidence intervals of the PV mean.

after clear-cuts (Palviainen et al., 2005). Lower sensitivity of this species to belowground damage was already pointed out by Vanha-Majamaa et al. (2017).

We recorded the appearance of new species in clear-cut plots of PV. The newcomers were more light-demanding when compared to semishade forest species like *V. vitis-idaea* and *V. myrtillus*. New herb species start to appear in the forest less than 2 years after the forest's disturbance. The spreading of such species depends on the long-term persistent seed bank or efficient wind dispersal (Pykälä, 2004; Haughian and Frego, 2016). We considered that the spreading of disturbed habitat species was also stimulated by seed dispersal type, i.e. anemochory (Appendix). *C. vulgaris* is definable as an ambophilous and anemochorous species, so these peculiarities could be a reason for the fast restoration by seedlings.

Humphrey and Coombs (1997) analyzed the effective protection of forest ecosystems and confirmed that maximization of diversity of plant species is also concerned with the conservation of sensitive, rare, and specialized species. We observed that clubmosses *L. clavatum* and *L. annotinum*, as well as *G. repens*, *A. uva-ursi*, and *C. majalis*, are intolerant to damage caused by clear-cut logging. Except *L. clavatum*, they are semishade forest species and did not survive in clear-cuts of PVM forest types. Although *L. clavatum* is considered a light-demanding plant and is rarely found in sites with relative summer illumination of less than 40% (Ellenberg et al., 1991), this species can be vulnerable to physical damage. If the mature plants of *L. clavatum* and *L. annotinum* disappear, recovery is questionable because the juvenile populations can only emerge in sites with limited disturbance (Rimgailė-Voicik and Naujalis, 2016). The aforementioned species of PV and

PVM forest types are the most sensitive to drastic changes of forest ecosystem after clear-cuts. This is also connected to their low frequency and cover. Such plant species can be protected by leaving uncut patches in a forest during logging (Graaf and Roberts, 2009).

Forest management also influences plant/pollinator interactions. Our study showed that clear-cut sites sustain larger pollinator assemblages than mature forests. As reported by Daubaras et al. (2017), who worked in the same experimental setting shortly after forest clearance, this increase in visitation may not be detectable in initial phases of forest regeneration. Later, the regeneration of ericaceous shrubs and the arrival of herb species may sustain higher pollinator diversity, as shown in Finnish forests, where significant positive effects on butterflies and bee abundance and diversity were observed mostly in the second year after disturbance and correlated with the flower and shrub coverage (Korpela et al., 2015). Similar increase was also detected in other studies (Taki et al., 2013; Nielsen and Totland, 2014); however, such effects may not be universal for all investigated species. For instance, Rodriguez and Kouki (2015) found that *V. myrtillus* performance and reproduction was higher in mature forests, whereas *V. vitis-idaea* benefited from disturbance regimes.

In conclusion, this study recorded the initial effects of forest disturbance on understory vascular plants caused by clear-cuts. The significant decline of Ericaceae shrub cover was shown for *Vacciniosa* and *Vaccinio-myrtillosa* forest types after clear-cuts. We conclude that clear-cut logging seriously destroys dwarf shrub populations in Scots pine-dominated forests. However, reactions and possibilities to restore different Ericaceae are species-

specific. For example, *V. vitis-idaea* is able to survive after clear-cut damages because the frequency of plants was defined as high enough in *Vaccinio-myrtillosa* forest plots after 2 years. The ability of this drought-resistant species to spread through underground rhizomes would promote its reproducibility. Nevertheless, the rhizomatous plant *V. myrtillus* demonstrated significantly stronger negative response in the cut forests. The forest-related endangered species *G. repens*, *A, uva-ursi*, and *L. annotinum* were indicated as the most vulnerable. Logging positively influenced the spread of *C. vulgaris* via seedlings, and the number of new annual and perennial herb species. This increase in floral diversity caused stimulated mutualistic interactions between our focus plants and their pollinators.

References

Andersson J, Dynesius M, Hjältén J (2017). Short-term response to stump harvesting by the ground flora in boreal clearcuts. Scand J Forest Res 32: 239-245.

Atlegrim O, Sjöberg K (1996). Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvest in uneven-aged boreal *Picea abies* forests. Forest Ecol Manag 86: 39-50.

Bergstedt J, Hagner M, Milberg P (2008). Effects on vegetation composition of a modified forest harvesting and propagation method compared with clear-cutting, scarification and planting. Appl Veg Sci 11: 159-168.

Clason AJ, Lidgren PMF, Sullivan TP (2008). Comparison of potential non-timber forest products in intensively managed young stands and mature/old growth forests in south-central British Columbia. Forest Ecol Manag 256: 1897-1909.

Daubaras R, Cesoniene L, Zych M, Tamutis V, Stakėnas V (2017). Effect of forest clear cuts on plant–pollinator interactions: the case of three ericaceous subshrubs in Lithuanian pine forests. Acta Agrobot 70: 1707.

Descamps CH, Moquet L, Migon, M, Jacquemart AL (2015). Diversity of the insect visitors on *Calluna vulgaris* (Ericaceae) in Southern France heathlands. J Insect Sci 15: 130.

Dufrêne M, Legendre P (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67: 345-366.

Ehlers T, Berch SM, MacKinnon A (2003). Inventory of non-timber forest product plant and fungal species in the Robson Valley. BC Journal of Ecosystems and Management 4: 1-15.

Ellenberg H, Weber H., Düll R, Wirth V, Werner W, Paulissen D (1991). Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18: 1-248 (in German).

Gilliam FS (2007). The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57: 845-856.

Graaf M, Roberts MR (2009). Short-term response of the herbaceous layer within leave patches after harvest. Forest Ecol Manag 257: 1014-1025.

Haughian SR, Frego KA (2016). Short-term effects of three commercial thinning treatments on diversity of understory vascular plants in white spruce plantations of northern New Brunswick. Forest Ecol Manag 370: 45-55.

Heinrichs S, Schmidt W (2009). Short-term effects on selection and clear cutting on the shrub and herb layer vegetation during the conversion of even-aged Norway spruce stands into mixed stands. Forest Ecol Manag 258: 667-678.

Hekkala AM, Tarvainen O, Tolvanen A (2014). Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. Forest Ecol Manag 330: 55-66.

Humphrey JW, Coombs EL (1997). Effects of forest management on understorey vegetation in a *Pinus sylvestris* L. plantation in NE Scotland. Botanical Journal of Scotland 49: 479-488.

Karazija S (2003). Age-related dynamics of pine forest communities in Lithuania. Baltic For 9: 50-62.

Korpela EL, Hyvonen T, Kuussaari M (2015). Logging in boreal field-forest ecotones promotes flower-visiting insect diversity and modifies insect community composition. Insect Conserv Divers 8: 152-162.

Lortie CJ, Budden A, Reid A (2011). From birds to bees: applying video observation techniques to invertebrate pollinators. J Pol Ecol 6: 125-128.

Luken JO (2003). Invasions of forests of the eastern United States. In: Gilliam FS, Roberts MR, editors. The Herbaceous Layer in Forests of Eastern North America. New York, NY, USA: Oxford University Press, pp. 283-301.

McCarthy BC (2003). The herbaceous layer of eastern old-growth deciduous forests. In: Gilliam FS, Roberts MR, editors. The Herbaceous Layer in Forests of Eastern North America. New York, NY, USA: Oxford University Press, pp. 163-176.

Ministry of the Environment (2016). Lithuanian Statistical Yearbook of Forestry. Kaunas, Lithuania: Public Company Lutute Publishing House.

Navasaitis M, Ozolinčius R, Smaliukas D, Balevičienė J (2003). Dendroflora of Lithuania. Kaunas, Lithuania: Lututė (in Lithuanian with a summary in English).

Nielsen A, Totland O (2014). Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. Oikos 123: 323-333.

Niemirski R, Zych M (2011). Fly pollination of dichogamous *Angelica sylvestris* (Apiaceae): how (functionally) specialized can a (morphologically) generalized plant be? Plant Syst Evol 294: 147-158.

Nybakken L, Selås V, Ohlson M (2013). Increased growth and phenolic compounds in bilberry (*Vaccinium myrtillus* L.) following forest clear-cutting. Scand J Forest Res 28: 319-330.

Paillet Y, Berges L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma RJ, De Bruyn L, Fuhr M, Grandin U et al. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv Biol 24: 101-112.

Palviainen M, Finér L, Mannerkoski H, Piirainen S, Starr M (2005). Responses of ground vegetation species to clear-cutting in a boreal forest: above-ground biomass and nutrient contents during the first 7 years. Ecol Res 20: 652-660.

Pykälä J (2004). Immediate increase in plant richness after clear-cutting of boreal herb-rich forests. Appl Veg Sci 7: 29-34.

Rimgailė-Voicik R, Naujalis J R (2016). Presence of juvenile club moss (Lycopodiaceae) sporophytes and gametophytes in relation to vegetation cover in dry pine forests. Am Fern J 106: 242-257.

Rodríguez A, Kouki J (2015). Emulating natural disturbance in forest management enhances pollination services for dominant *Vaccinium* shrubs in boreal pine-dominated forests. Forest Ecol Manag 350: 1-12.

Spiecker H (2003). Silvicultural management in maintaining biodiversity and resistance of forests in Europe-temperate zone. J Environ Manag 67: 55-65.

Taki H, Okochi I, Okabe K, Inoue T, Goto H, Matsumura T, Makino S (2013). Succession influences wild bees in a temperate forest landscape: the value of early successional stages in naturally regenerated and planted forests. PLoS One 8: e56678.

Tonteri T, Salemaa M, Rautio P, Hallikainen V, Korpela L, Merilä P (2016). Forest management regulates temporal change in the cover of boreal plant species. Forest Ecol Manag 381: 115-124.

Vanha-Majamaa I, Shorohova E, Kushnevskaya H, Jalonen J (2017). Resilience of understory vegetation after variable retention felling in boreal Norway spruce forests – A ten year perspective. Forest Ecol Manag 393: 12-28.

Zych M, Michalska B, Krasicka-Korczyńska E (2014). Myophily in the critically endangered umbelliferous plant *Ostericum palustre* Besser (Apiaceae). Plant Syst Evol 300: 187-196.

Zych M, Stpiczynska M, Roguz K (2013). Reproductive biology of the Red List species *Polemonium caeruleum* (Polemoniaceae). Bot J Linn Soc 173: 92-107.

Appendix. Characteristic of pollination and seed (spore) dispersal of understory plant species.

	Pollination system	Main pollen vectors	Seed (spore) dispersal (chory)	References
Vaccinium vitis-idaea	Zoophily	Bees	Zoochory	Jacquemart, 1997
Vaccinium myrtillus	Zoophily	Bees, flies	Zoochory	Jacquemart, 1997
Festuca ovina	Anemophily		Anemochory	Wilson and Thompson, 1989
Calluna vulgaris	Ambophily	Bees, flies	Anemochory	Descamps et al., 2015
Solidago virgaaurea	Zoophily	Bees, flies	Anemochory	Akiko and Koichi, 2017
Arctostaphyllos uva-ursi	Zoophily	Bees, thrips	Zoochory	García-Fayos and Goldarazena, 2008
Lycopodium clavatum			Anemochory	Mabberley, 2008
Luzula pilosa	Anemophily		Anemochory	Mabberley, 2008
Pilosella officinarum	Autogamy/apomictic		Anemochory	Bishop and Davy, 1994
Calamagrostis epigeios	Anemophily		Anemochory	Mabberley, 2008
Rumex acetosella	Anemophily		Anemochory	Knuth, 1899
Carex sp.	Anemophily		Autochory	Mabberley, 2008
Senecio vulgaris	Zoophily	Bees, flies, beetles	Anemochory	Kadereit, 1984
Epilobium angustifolium	Zoophily	Bees, butterflies	Anemochory	Schmid-Hempel and Speiser, 1988
Veronica officinalis	Zoophily	Bees, flies, butterflies	Autochory	Knuth, 1899
Corynephorus canescens	Anemophily		Autochory	Mabberley, 2008
Spergula arvensis	Autogamy/zoophily	Flies	Autochory	New, 1961
Melampyrum pratense	Zoophily	Bees	Myrmecochory	Kwak and Jennersten, 1991
Convallaria majalis	Zoophily	Bees	Autochory	Knuth, 1899
Trientalis europaea	Zoophily	Bees, flies	Autochory	Taylor et al., 2002
Lycopodium annotinum			Anemochory	Mabberley, 2008
Goodyera repens	Zoophily	Bees	Anemochory	Brzosko et al., 2013

Additional references

Akiko S, Koichi T (2017). Flowering phenology and reproduction of the *Solidago virgaurea* L. complex along an elevational gradient on Mt Norikura, central Japan. Plant Species Biol 32: 270-278.

Bishop GF, Davy AJ (1994). *Hieracium pilosella* L. (*Pilosella officinarum* F. Schultz & Schultz-Bip.). J Ecol 82: 195-210.

Brzosko E, Wróblewska A, Jermakowicz E, Hermaniuk A (2013). High level of genetic variation within clonal orchid *Goodyera repens*. Plant Syst Evol 299: 1537-1548.

Descamps C, Moquet L, Migon M, Jacquemart AL (2015). Diversity of the insect visitors on *Calluna vulgaris* (Ericaceae) in Southern France heathlands. J Insect Sci 15: 130.

García-Fayos P, Goldarazena P (2008). The role of thrips in pollination of *Arctostaphyllos uva-ursi*. Int J Plant Sci 169: 776-781.

Jacquemart AL (1997). Pollen limitation in three sympatric species of *Vaccinium* (Ericaceae) in the Upper Ardennes, Belgium. Plant Syst Evol 207: 159-172.

Kadereit JW (1984). The origin of *Senecio vulgaris* (Asteraceae). Plant Syst Evol 145: 135-153.

Knuth P (1899). Handbuch der Blütenbiologie, II Band, 2. Teil: Lobeliaceae bis Gnetaceae. Leipzig, Germany: Verlag von Wilhelm Engelmann (in German).

Kwak MM, Jennersten O (1991). Bumblebee visitation and seedset in *Melampyrum pratense* and *Viscaria vulgaris*: heterospecific pollen and pollen limitation. Oecologia 86: 99-104.

Mabberley DJ (2008). Mabberley's Plant-Book. A Portable Dictionary of Plants, Their Classification and Uses. 3rd ed. Cambridge, UK: Cambridge University Press.

New JK (1961). *Spergula arvensis* L. J Ecol 49: 205-215.

Schmid-Hempel P, Speiser B (1988). Effects of inflorescence size on pollination in *Epilobium angustifolium*. Oikos 53: 98-104.

Taylor K, Havill DC, Pearson J, Woodall J (2002). *Trientalis europaea* L. J Ecol 90: 404-418.

Wilson AM, Thompson K (1989). A comparative study of reproductive allocation in 40 British grasses. Funct Ecol 3: 297-302.