

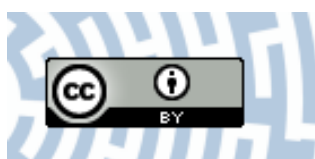


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Author: Anna Orczewska, Patryk Czortek, Bogdan Jaroszewicz

Citation style: Orczewska Anna, Czortek Patryk, Jaroszewicz Bogdan. (2019). The impact of salvage logging on herb layer species composition and plant community recovery in Białowieża Forest. "Biodiversity and Conservation" (15 Jun 2019), doi 10.1007/s10531-019-01795-8



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The impact of salvage logging on herb layer species composition and plant community recovery in Białowieża Forest

Anna Orczewska¹ · Patryk Czortek² · Bogdan Jaroszewicz²

Received: 26 September 2018 / Revised: 18 March 2019 / Accepted: 6 June 2019
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Abstract

Białowieża Forest is one of the closest to pristine forest ecosystems in temperate vegetation zone in European Lowland, which is still being transformed by forest management. We investigated the effects of salvage logging of spruce stands killed by bark beetle on the recovery process and the biodiversity of the herb layer in the early stages of vegetation development after felling, on the habitat of mixed deciduous, oak-lime-hornbeam forest (*Tilio-Carpinetum*). We tested: (i) to what extent salvage logging modifies the plant species richness and diversity compared to sites left intact; (ii) whether clear-felling leads to an increase in diversity of vascular plants; and (iii) which ecological groups of plants benefit, and which are hindered by disturbance, depending on age and size of the clear-felled site. Salvage harvesting executed between 2012 and 2016 led to an increase in overall plant diversity. However, the winners were the species of open habitats, promoted by soil disturbance, whereas the number and cover of ancient forest indicator species decreased in comparison to unlogged forests. Both trends were significantly related to the increasing size of clear-felled sites, and developed right after logging. A comparison of the species composition of the disturbed (logged and unlogged) sites with undisturbed forest with stands unaffected by infestation, treated as control plots revealed the great potential of the affected sites for spontaneous recovery towards the oak-lime-hornbeam forest community, despite 50–90 years of spruce-dominated stand cover. We conclude that continuous deterioration of the forest habitats via clearcutting of stands affected by insect outbreak, followed by tree planting, substantially reduces the chances of successful, natural regeneration towards deciduous, structurally complex and diverse forests.

Keywords Norway spruce · Bark beetle outbreak · Clearcutting · Natural disturbance · Biodiversity

Communicated by Daniel Sanchez Mata.

This article belongs to the Topical Collection: Forest and plantation biodiversity.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10531-019-01795-8>) contains supplementary material, which is available to authorized users.

Extended author information available on the last page of the article

Introduction

Biotic and abiotic disturbances are part of the dynamics of pristine forests (Fischer et al. 2013). They increase the structural and biological diversity of forests, both in time and space (Fischer 2011; Lehnert et al. 2013; Winter et al. 2015). Norway spruce (*Picea abies* (L.) H. Karst) dominated stands of Central Europe are frequently affected by outbreaks of *Ips typographus* L.—the European spruce bark beetle (Lewis and Lindgren 2000; Martikainen et al. 1999; Nilsson 1997; Schulze et al. 2005; Shorohova et al. 2009), which often initiates “stand replacement” pathways of forest regeneration (sensu Veblen 1992).

Such large scale disturbance-driven processes of forest stand dynamics are difficult to accept from the economic point of view. Thus, stands killed by insect outbreaks are usually salvage logged and replanted, while natural processes leading to forest regeneration play a minor role. Meanwhile, natural disturbances, such as bark beetle outbreak, are spatially and temporarily heterogeneous, which leads to more diverse and structurally complex forest, often composed of trees with natural, genetically inherited resistance to beetle attacks (Six et al. 2018; Žmihorski et al. 2018). Outbreaks enhance key ecological processes, and in turn facilitate high diversity of many functional groups of organisms (Beudert et al. 2015; Lindenmayer and Noss 2006; Mikusiński et al. 2018; Winter et al. 2015). In contrast, the sanitary/salvage logging (commercial tree harvesting, from sites affected by disturbance) and planting of trees on sites affected by disturbances substantially reduce understory cover and richness (Fischer and Fischer 2009; Ruben et al. 1999; Titus and Householder 2007) and temporarily hamper the recovery of forest plant species. In European forests, clearcutting followed by tree planting often in understory and herbaceous vegetation leads to the dominance of plants from *Rubus* or *Calamagrostis* genera (Fischer and Fischer 2009), or dominance of other species which may temporarily inhibit the further stages of forest succession (sensu Connell and Slatyer 1977). Consequently, human intervention via extraction of trees and successive planting of a new generation of trees inhibits post-disturbance ecosystem restoration, since it interferes with natural processes, such as hydrological regimes, nutrient cycling (promotes soil erosion and soil nutrient loss instead), natural regeneration of trees and herb layer recovery. Thus, the human “clean-up” attitude inevitably leads to the homogenization of the forest structure (Lindenmayer and Noss 2006; Lindenmayer et al. 2017; Thorn et al. 2017; Titus and Householder 2007). Due to excessive soil disturbance and increase of light, it promotes the establishment of early-successional, light-demanding, ruderal and invasive species (Collins and Pickett 1988a; Kusumoto et al. 2015; Moola and Vasseur 2008; Odor et al. 2018; Rumbaitis-del Rio 2006).

According to the gap dynamics model (e.g. Bobiec et al. 2000), the general pattern of the understory flora reaction to natural canopy opening includes the early-successional phase, composed of light-demanding, competitive, nitrophilous plants, which are gradually replaced by late-successional, shade-tolerant species (Faliński 1986). In contrast to the size of natural gaps in the tree canopy of mixed deciduous forests (Bobiec et al. 2000), post-disturbance logging creates much bigger open areas (Mikusiński et al. 2018). Although clearcutting often leads to a temporary increase in understory plant species richness due to the early-successional species, this peak disappears after 1–10 (15) years, mostly as a result of tree canopy closure (Duguid and Ashton 2013; Hannerz and Hånell 1997). Meanwhile, shade-tolerant, late-successional plants typical of old-growth forests often disappear or reduce their abundance due to heavy disturbance caused by the logging operations (Jonášová and Prach 2008; Moola and Vasseur 2008; Swanson et al. 2011).

Białowieża Forest (BF), located in the borderland of Poland and Belarus, is one of the most pristine European forest complexes. It possesses great conservation value due to its high biological diversity of forest communities and high share of old-growths of natural origin still shaped by natural disturbance (including bark beetle outbreaks) (Faliński 1986). It has maintained its natural character because commercial forestry was implemented there only 100 years ago. Prior to World War I, tree cutting in BF was very occasional and usually not followed by any type of artificial forest regeneration (Genko 1902, 1903; Kartsov 1903). This makes BF unique in comparison with other lowland forest complexes in Europe, since a substantial proportion of it still originates from natural regeneration. Since 2014, almost 100% of BF on the Polish side of the national border, including commercial forest stands managed by Polish National Forest Holding “State Forests”, is covered by the Natura 2000 site and the transboundary UNESCO World Heritage Site “Białowieża Forest”. Thus, BF is regarded as a biodiversity hot-spot and an area of high conservation value where the overall goal is to protect natural processes, forest dynamics and biodiversity of forest species. Consequently, such conservation status implies serious restrictions in forest management and timber exploitation (Kujawa et al. 2016).

Despite the high level of BF naturalness, expressed in species composition of stands well reflecting habitat conditions (Faliński 1986), the area managed by the National Forest Holding is covered by an artificially high share of planted stands dominated by Norway spruce and Scots pine *Pinus sylvestris* (27% and 26% respectively) (Biuro Urządzenia Lasu i Geodezji Leśnej, unpubl.). This is the legacy of former forest management (clearcutting followed by planting), which promoted conifer stands (predominantly planted 70–90 years ago) at the cost of *inter alia* oak-lime-hornbeam mixed deciduous forests of the *Tilio-Carpinetum* type.

During the last 6 years (2012–2018) BF has witnessed one of the most severe outbreaks of spruce bark beetle since the beginning of the twentieth century, which most severely affected the spruce-dominated stands planted on the sites where natural potential vegetation would be dominated by broadleaved trees. Despite the UNESCO World Heritage status, forest managers decided to implement salvage logging followed by tree planting rather than leaving disturbed areas for natural recovery. There is great disagreement between resource managers and conservationists concerning the necessity and effectiveness of implementation of salvage logging to combat the insect outbreaks. It is questioned especially in the case of protected areas (Hagge et al. 2018; Müller et al. 2018; Thorn et al. 2017). It has been widely practiced in forestry since the nineteenth century as a standard treatment after insect infestations (Więcko 1984). Lindenmayer et al. (2004) claim that it is implemented by policy-makers and forest managers, who have a poor understanding of the value of natural disturbances in the restoration of structural complexity and diversity in forests, which once lost such features due to previous management practices.

We investigated the consequences of clearcutting (cutting all the trees) on species composition and the diversity of the herbaceous layer. We envision the documentation of post-logging vegetation changes in BF as important information since it might assist future restoration efforts attempted in this unique forest and other forest complexes maintaining high conservation value. We selected the forest floor species since they reflect habitat conditions and are good indicators of disturbance, because they react to it quicker than trees and shrubs (Gilliam and Roberts 2003; Mayer et al. 2004). Thus, they can be a good predictor of the possible future forest succession pathways. In the light of the current knowledge on the effects of post-disturbance logging on plant species composition and forest regeneration, we expected that: (i) salvage logging contributed to an increase in biotic diversity of the vascular, herb layer plants and promoted the richness and cover of early-successional,

shade-intolerant species but hindered species associated with forest interiors; (ii) the bigger the size of the clear-felled sites the more severe the alterations to the herbaceous vegetation are observed.

Materials and methods

Study area and data collection

The study was carried out in mid-late June 2016 and in early July 2017, in the commercial part of the BF (52°30′–53° N, 23°30′–24°15′ E), in sites occupied by spruce-dominated forests originating from planting, on the habitat of the species-rich oak-lime-hornbeam mixed deciduous forest—*Tilio-Carpinetum* community. The *Tilio-Carpinetum* community is characterized by two distinct phenological aspects: the spring one dominated by light-demanding, vernal geophytes and the consecutive summer aspect appearing at the end of May, mainly composed of shade-tolerant hemicryptophytes (Faliński 1986). A slight shift in inventory times (June vs. July), which was the effect of logistic problems in the course of the study, should not have negative implications on the cover differences of individual species between these dates since these periods represent the same phenological aspect of vegetation. The studied stands, mostly planted in the 1920s on sites logged by the Century European Timber Corporation (Bajko 2001), are the most heavily affected by the recent bark beetle outbreak. Current infestation is very severe; so far it has affected (killed) ca. 31% of the volume of spruce trees (unpublished data available from P. Chylarecki, calculated based on data obtained from the Regional Forest Directorate in Białystok and the Forest Management Plan for 2012–2021, for the area of BF outside the Białowieża National Park).

In order to allow the before-after control-impact study design of the total 89 research plots which we selected for the vegetation study, 30 were located on 11 areas where stands killed by bark beetle were clear-felled and wood was extracted (logged), 28 in the forests with dead standing spruce treated as a reference of pre-harvest conditions (unlogged sites) and 31 in the uncut, alive forest stands, dominated by broadleaved species with an admixture of Norway spruce, unaffected by bark beetle, treated as control. In the majority of cases the control plots were adjacent to the clear-felled sites. However, it was not the rule with the dead unlogged stands since in some cases they were not available in direct proximity of the logged sites. In such situations we selected the dead spruce-dominated plots as close to the remaining sites as possible, bearing in mind that they should occupy the same *Tilio-Carpinetum* forest habitat type (selected on the basis of forest habitat maps). All three site types were located within moderately humid habitats, of either high or moderate fertility (broadleaved fresh forest and broadleaved mixed fresh forest, according to Polish forest habitat classification, respectively). In natural conditions such sites should be occupied by the *Tilio-Carpinetum* community. All the plots were situated within the part of BF managed by the State Forests administration (Fig. 1).

We investigated all the clear-felled sites which were available in 2016 in the pool of such sites within the broadleaved and mixed-broadleaved forest habitats. In all sites, trees were logged with chain saws, then extracted with skidders, whereas the remaining logging slash was piled on the borders of the clear-felled areas (Online Resource 1). Most of the clear-felled areas represented the initial stages of forest post-disturbance salvage-logging regeneration with very low cover of woody plants (0–1%), which survived felling and

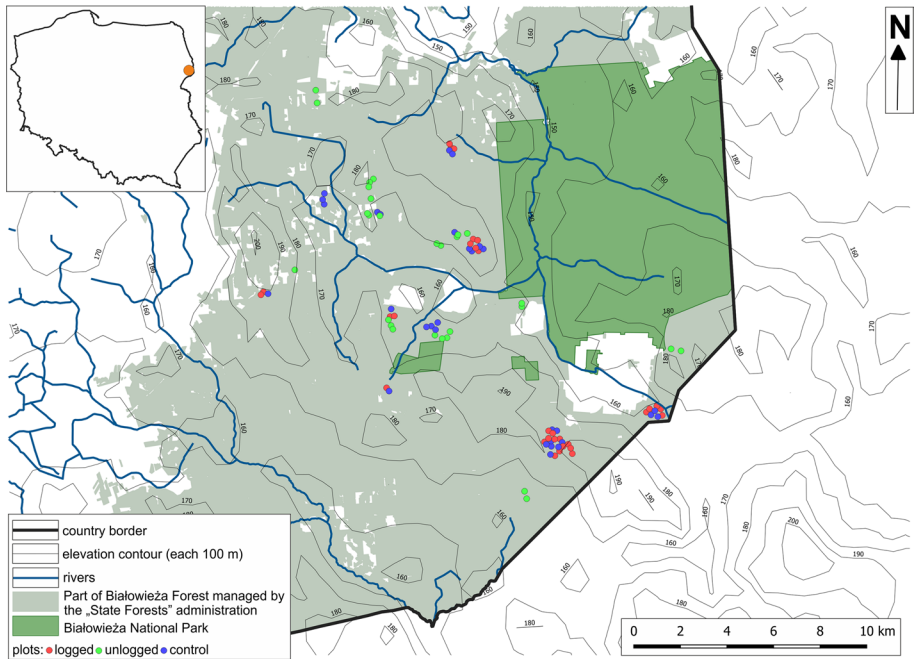


Fig. 1 Location of the study plots

tree-removal operations, with *Tilia cordata*, *Carpinus betulus*, and *Corylus avellana* being the most frequent. In five cases, removal of felled trees had not yet been followed by tree planting, whereas, in the remaining six sites, either *Quercus robur*, *T. cordata*, *Picea abies*, *P. sylvestris*, or/and *Malus* sp. were planted (currently still occurring in the herb layer). The approximate time of logging ranged from the period 2012–2015 (the result of successive, imposed salvage logging, conducted in winter and spring, that led to the presence of large openings in the forest—age class: old; 1–5 years after felling) through autumn 2015 to winter and spring 2016 (age class: young; 0 yrs after felling). The size of the clear-felled areas varied from 0.162 to 2.85 ha, influencing the number of research plots (10 × 10 m) set in each study site, i.e. from one plot on the smallest to five randomly located plots on the largest clear-felled sites (the number of plots in each site is given in Table 1). In each plot we estimated the individual percentage cover of all vascular plant species in the herb layer according to the following scale: 1%, 5%, 10%, and then at 10% intervals.

To determine plant species' ecological requirements for light (EIV-L), soil moisture (EIV-M), nitrogen (EIV-N, indicator corresponding to plant productivity) and soil reaction (EIV-R) we used Ellenberg's ecological indicator values (Ellenberg et al. 1991). We also compared the Shannon diversity index, the number and total cover of plant species of open habitats, and the number and cover of ancient woodland indicator species sensu Peterken (1974) in modification of Dzwonko and Loster (2001), across the three site types studied. Ancient woodland indicator species are a good proxy of forest habitat conditions since they are mostly associated with forest interiors, whereas their distribution outside forests and in heavily disturbed forests is very limited (Hermy et al. 1999). As light-demanding species mostly associated with open habitats and indicating disturbance we assumed those typical to seminatural shrub communities (*Rhamno-Prunetea*), meadows

Table 1 General description of clear-felled sites studied

Site id	Forest division	Location GPS		Plot number	Area (ha)	Habitat type	Clear-felled site age class	Tree species planted
		N	E					
S1	280Da	52.752918	23.776988	1,2,3,28,30	2.85	FB	Old	QR
S2	156Ca	52.790513	23.766002	4,5,6,29	1.62	FMB	Young	QR
S3	498Ci/526Ab	52.675237	23.814282	7,8,9,10	1.27	FMB	Old	QR, BP, PA,
S4	526Ba/526Bb	52.674612	23.824281	11	0.21	FMB	Young	-
S5	526Ba	52.673884	23.826770	12,13	1.01	FMB	Old	-
S6	526Ba/526Bb	52.672426	23.827114	14,15	0.181	FMB	Old	QR
S7	526Bb/526Ba	52.670917	23.821964	16,17	1.33	FMB	Young	-
S8	331Ab	52.739721	23.640947	18,19	0.529	FMB	Young	PS, TC
S9	502Ed/502Eh	52.682418	23.889169	20,21,22,23,24	0.959	FB	Young	QR, TC
S10	444Da	52.698753	23.714761	25	0.362	FB	Old	QR, MS, PA
S11	363Ao	52.727040	23.720254	26,27	0.162	FB	Young	-

Habitat type: *FB* fresh broadleaved forest, *FMB* fresh mixed-broadleaved, clear-felled site age class: *young* autumn 2015 till winter/early spring 2016, *old* successive, imposed salvage logging between 2012 and 2015, tree species planted: *QR* *Quercus robur*, *BP* *Betula pendula*, *PA* *Picea abies*, *PS* *Pinus sylvestris*, *TC* *Tilia cordata*, *MS* *Malus* sp.

(*Molinio-Arrhenatheretea*), ruderal and segetal tall herbs (*Artemisietea vulgaris* and *Stellarietea mediae*). To determine the affiliation of plant species to the phytosociological classes, we used the classification of plant communities by Ratyńska et al. (2011). The nomenclature of vascular plants followed Euro+Med (2006), whereas ancient forest indicator species were distinguished following the list given for Poland by Dzwonko and Loster (2001).

Data analysis

To detect the dissimilarities in species composition between logged, unlogged and control sites, for each plot we calculated the Bray–Curtis dissimilarity index (based on species' abundance data), then applied a hierarchical clustering (Ward's minimum variance method). To analyse vegetation patterns and relationships between variables describing plant species composition across the three groups of site, we performed a Detrended Correspondence Analysis (DCA). To reduce the impact of species that occurred in low abundance (<5%) on the ordination results, the downweighting of rare species was applied prior to the DCA analysis. Weighted mean values of ecological indicators (EIV), Shannon–Wiener diversity index, as well as the number and total cover of all plant species recorded in the three site types analysed were fitted as passive vectors to the ordination results, plotted as a DCA biplot. In this analysis, with the exception of the total species richness and cover, we also included the number and cover of plant species associated with open habitats and the number and cover of ancient woodland indicator species. For each vector, we calculated the determination coefficient R^2 and p value, using a permutation test with 999 iterations.

We used ANOVA to compare the proportions of species with different ecological requirements for light, moisture, nitrogen and reaction, for the Shannon–Wiener index, the total number and cover of the herb layer species, and the number and cover of species typical to open habitats and ancient woodland indicator species across the three vegetation types surveyed. To check whether there were significant differences among the logged, unlogged and control forests in respect to the above-mentioned variables, we used a post hoc Tukey test.

In the next step, we compared the frequency (number of plots where species occurred) and cover (total cover of species in each plot category) of all the herb layer species in logged, unlogged and control sites, using the non-parametric ANOVA with a post hoc test for multiple comparison of treatments, and the criterion of Fisher's least significant difference. To avoid the effect of rare species, following the conventional rule of thumb, in this procedure we analysed species recorded at least five times and with the total cover higher than 5% in at least one of the site types compared. In effect, the number of species used to calculate the frequency differences was reduced from 203 to 93, whereas in the case of differences in species abundance the pool included 105 species. Special attention was paid to species which (i) were significantly associated with forest unaffected by bark beetle (control), (ii) were sensitive to clear-felling since they avoided clear-felled areas, and had higher frequency and cover in forests (control or unlogged), or (iii) showed a distinctive preference for logged sites, where their number and cover was the highest. To determine whether the time since clearcutting (age of logged sites) and the size of logged sites influenced changes in the number and total cover of species of open, disturbed habitats, and of the ancient woodland indicator species, we used linear regression. In order to avoid biases connected with the uneven ranges among variables and to reduce skewness, data were scaled, centered and transformed using Yeo-Johnson power transformations (Yeo and

Johnson 2000). All statistical analyses were performed using R software (R Core Team 2017) and the significance of results was evaluated at $p=0.05$.

Results

The hierarchal clustering analysis based on the Bray–Curtis dissimilarity index revealed a low level of compositional dissimilarities between unlogged and control plots, whereas the magnitude of dissimilarities between logged and the two remaining groups of study sites (unlogged and control forests) was distinctive (Fig. 2). Detrended Correspondence Analysis showed distinct differences in species composition between the logged sites and both remaining types of plot, while control and unlogged forest sites overlapped entirely (Fig. 3). The main factors explaining the diversity of species within plots representing logged sites were high values of light ecological indicator, Shannon–Wiener index, total species richness and total herb layer species cover, as well as the number and cover of species typical to open, disturbed habitats (Fig. 3; Table 2). Almost all of these variables were strongly positively associated with each other. In contrast, the species composition of control and unlogged forests was characterized by low values of all the above-mentioned vectors but a high value of the vector representing cover of ancient woodland indicator species (Fig. 3; Table 2).

The light requirement of species significantly differed among the site types. On logged sites there were more light-demanding species, whereas in unlogged and control forests

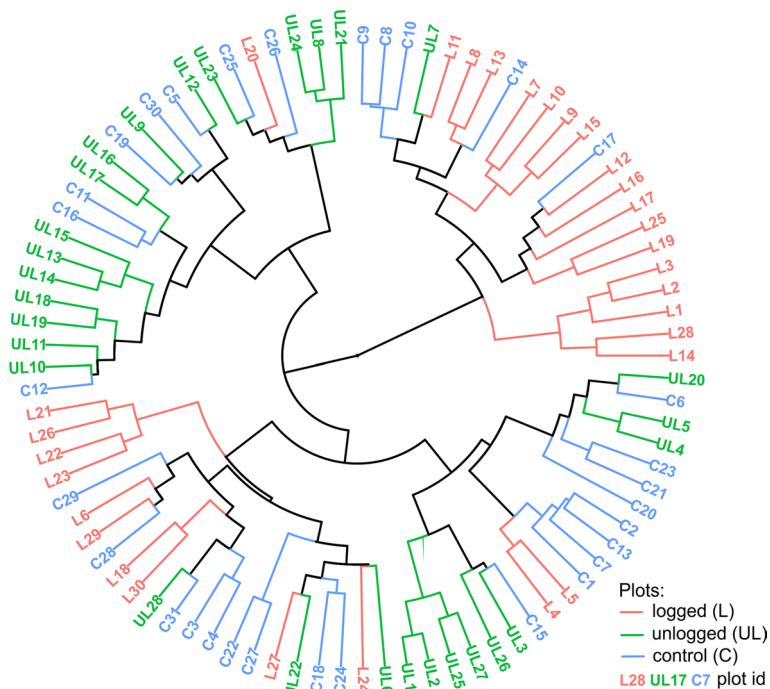


Fig. 2 Results of hierarchical clustering analysis with a criterion of Ward's minimum variance showing the Bray–Curtis compositional dissimilarities between vegetation types studied

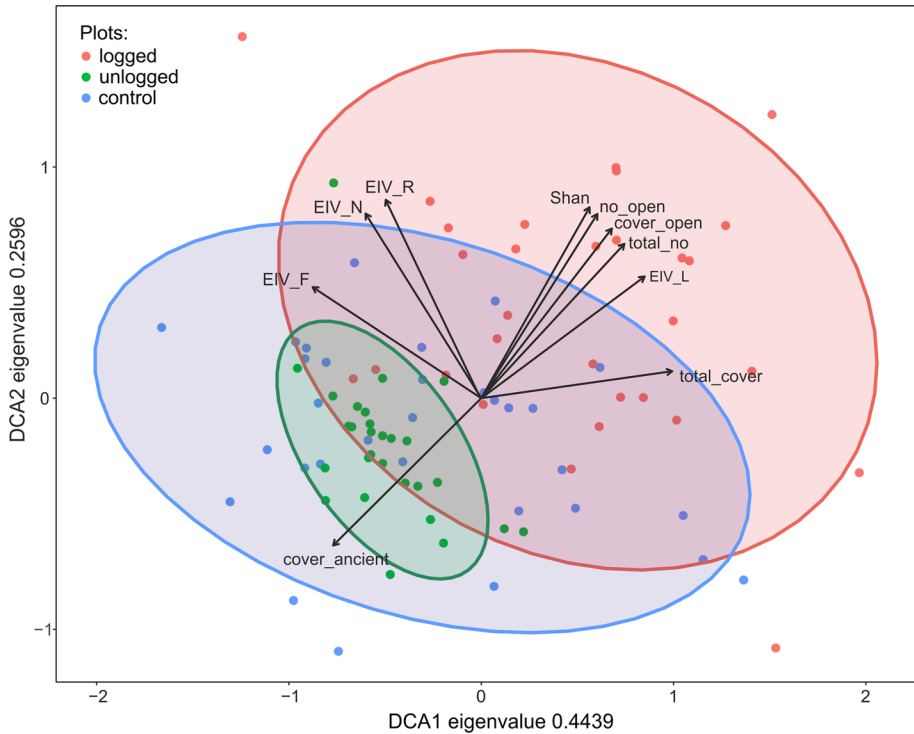


Fig. 3 Results of detrended correspondence analysis (DCA) showing the differences in species composition between clear-felled sites (logged) (n=30), forests with standing dead spruce (unlogged) (n=28) and unaffected forests (control) (n=31). Points represent sites. Ellipses represent 95% confidence levels. Arrows represent variables fitted to the DCA analysis results: EIV_L—light EIV, EIV_F—soil moisture EIV, EIV_R—soil reaction EIV, EIV_N—nitrogen EIV, Shan—Shannon–Wiener index, total_no and total_cover—total number and cover of species, no_open and cover_open—number and total cover of open-habitat species, cover_ancient—total cover of ancient woodland indicator species

Table 2 Parameters of variables passively fitted to the DCA ordination results

Parameter	Abbreviation	DCA1	DCA2	R ²
Light EIV	EIV_L	0.850	0.526	0.764***
Moisture EIV	EIV_F	-0.877	0.480	0.284***
Nitrogen EIV	EIV_N	-0.601	0.798	0.559***
Reaction_EIV	EIV_R	-0.526	0.850	0.196**
Shannon–Wiener index	Shan	0.563	0.826	0.301***
Total number of species	Total_no	0.744	0.667	0.306***
Cover of herb layer	Total_cover	0.993	0.116	0.213***
Number of open-habitat species	No_open	0.604	0.797	0.619***
Cover of open-habitat species	Cover_open	0.679	0.733	0.644***
Number of ancient woodland species	No_ancient	-0.509	0.860	0.005 n.s.
Cover of ancient woodland species	Cover_ancient	-0.770	-0.637	0.254***

Stars in the last column indicate statistical significance of results: ****p* < 0.001; n.s. not significant

EIV ecological indicator value (Ellenberg et al. 1991)

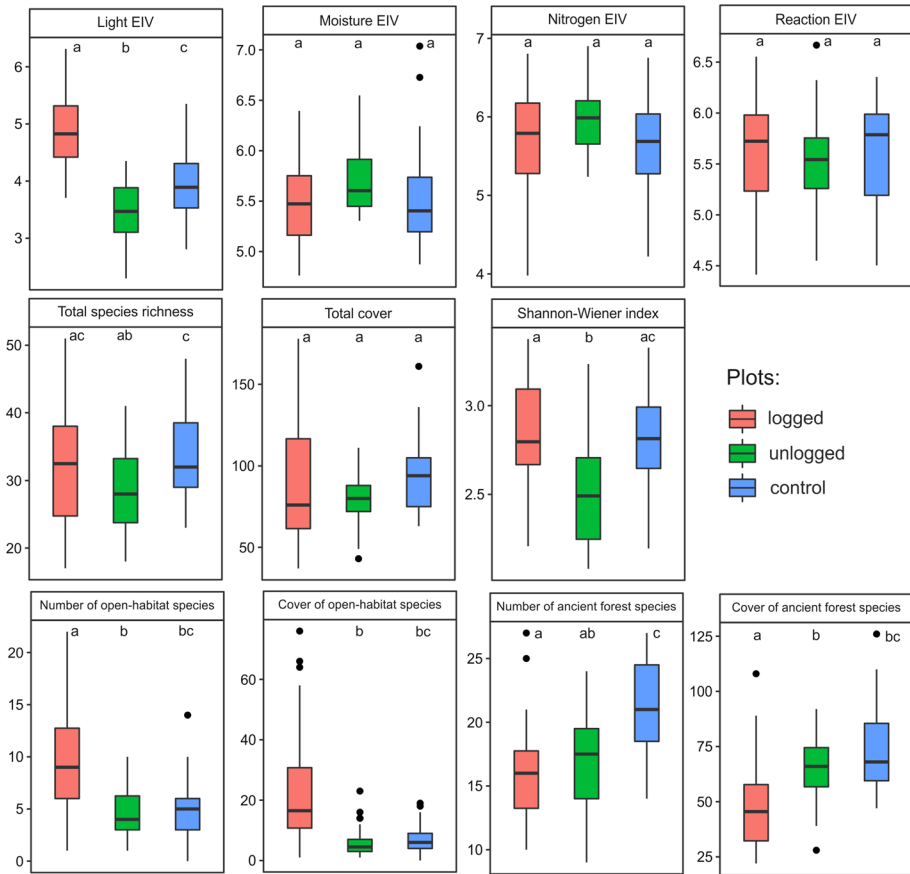


Fig. 4 Differences in mean values of the light, moisture, reaction and nitrogen EIVs, Shannon–Wiener index, total number of species, total cover of species, number and total cover of open-habitat species and ancient woodland indicator species between clear-felled sites (logged), forests with standing dead spruce (unlogged) and unaffected forests (control). The box covers the 95% confidence range. The thick horizontal line is the median. Black points are outliers. Letters show significance of results from the post hoc Tukey test

shade-tolerant ones predominated (Fig. 4). In the case of unlogged forests we documented significantly lower values of Shannon–Wiener index than in logged and control sites. Species richness was significantly higher in the control forests unaffected by bark beetle than in unlogged ones. Both the number and cover of species typical for open habitats were higher on logged sites than in the other types of site. The number of ancient woodland indicator species was significantly higher in control forests than in logged and unlogged stands, while their total cover was higher in both control and unlogged forests compared to logged sites. No significant differences amongst the three types of site were found for moisture, nitrogen and reaction EIV values, or for the total cover of herbaceous layer.

Of the 93 and 105 plant species taken into account, 35 showed significant differences in frequency and 41 in abundance amongst the three vegetation types analysed (Table 3). Five species: *Abies alba*, *Lilium martagon*, *Melittis melissophyllum*, *Prunus* sp. and *Sanicula europaea*, showed affinity with control forests and avoided sites with

Table 3 Comparison of species' frequency and abundance among the three site types surveyed. Kruskal–Wallis Chi^2 statistics calculated from non-parametric ANOVA are shown (Chi^2)

Species	Frequency			Cover			Significance	KW Chi^2	p	Significance											
	Logged	Unlogged	Control	Logged	Unlogged	Control															
	na	na	na	na	na	na															
More in control forest than in unlogged and logged sites; non-significant differences between unlogged and logged sites																					
<i>Abies alba</i>	0	0	4	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
<i>Lilium martagon</i>	0	1	9	15.11	<0.001	b	a	0	1	9	15.11	<0.001	b	a	8	7.74	0.020	b	b	a	
<i>Melittis melissophyllum</i>	3	2	15	18.19	<0.001	b	a	3	2	24	18.39	<0.001	b	a	9	15.11	<0.001	b	b	a	
<i>Prunus domestica</i>	0	0	5	9.80	0.007	b	a	0	0	5	9.80	0.007	b	a	5	9.80	0.007	b	b	a	
<i>Sanicula europaea</i>	3	5	14	11.03	0.004	b	a	3	5	18	11.28	0.003	b	a	18	11.28	0.003	b	b	a	
Less on logged sites than in unlogged and control forest; non-significant differences between unlogged and control forest																					
<i>Acer platanoides</i>	4	18	17	17.421	>0.001	b	a	4	18	17	17.421	>0.001	b	a	17	17.421	<0.001	b	a	a	
<i>Anemone nemorosa</i>	29	28	31	1.966	0.374	a	a	153	315	365	20.862	<0.001	b	a	365	20.862	<0.001	b	a	a	
<i>Cardamine bulbifera</i>	3	11	13	8.805	0.012	b	a	12	27	34	8.318	0.015	b	a	34	8.318	0.015	b	a	a	
<i>Galium odoratum</i>	11	20	21	8.804	0.012	b	a	11	79	70	12.845	0.001	b	a	70	12.845	0.001	b	a	a	
More on logged sites than in unlogged and control forest; non-significant differences between unlogged and control forest																					
<i>Agrostis gigantea</i>	11	0	1	20.746	>0.001	a	b	103	0	1	21.136	<0.001	a	b	1	21.136	<0.001	a	b	b	
<i>Carex leporina</i>	11	0	3	15.823	<0.001	a	b	15	0	3	15.928	<0.001	a	b	3	15.928	<0.001	a	b	b	
<i>Cenastium fontanum subsp. vulgare</i>	7	0	0	14.773	<0.001	a	b	7	0	0	14.773	<0.001	a	b	0	14.773	<0.001	a	b	b	
<i>Juncus tenuis</i>	5	0	0	10.301	0.005	a	b	13	0	0	10.293	0.005	a	b	0	10.293	0.005	a	b	b	
<i>Moehringia trinervia</i>	27	22	23	2.578	0.275	a	a	127	35	48	13.265	0.001	a	b	48	13.265	0.001	a	b	b	
<i>Myosoton aquaticum</i>	7	0	0	14.773	<0.001	a	b	7	0	0	14.773	<0.001	a	b	0	14.773	<0.001	a	b	b	
<i>Ochlopoa annua</i>	5	0	0	10.301	0.005	a	b	5	0	0	10.301	0.005	a	b	0	10.301	0.005	a	b	b	
<i>Poa trivialis</i>	10	2	2	10.464	0.005	a	b	22	2	2	10.951	0.004	a	b	2	10.951	0.004	a	b	b	
<i>persicaria hydropiper</i>	6	0	1	9.301	0.009	a	b	6	0	1	9.301	0.009	a	b	1	9.301	0.009	a	b	b	
<i>Rubus caesius</i>	26	0	2	63.524	<0.001	a	b	58	0	2	62.999	<0.001	a	b	2	62.999	<0.001	a	b	b	

Table 3 (continued)

Species	Frequency				Cover				Signifi- cance			
	Logged		Unlogged		Logged		Unlogged			Control	KW Chi^2	p
	Logged	Unlogged	Control	Unlogged	Logged	Unlogged	Control	Unlogged				
<i>Stellaria media</i>	17	2	3	2	56	2	12	24.751		<0.001	a b b	
<i>Stellaria palustris</i>	7	0	0	0	16	0	0	14.761		<0.001	a b b	
<i>Veronica chamaedrys</i>	20	10	10	10	32	10	10	10.196		0.006	a b b	
<i>Veronica officinalis</i>	19	3	4	3	44	3	4	26.689		<0.001	a b b	

Only species that showed significant differences in the number of occurrence or abundance are shown. Bold—significant results

Logged clear-felled sites, *unlogged* forest with standing dead spruce, *control* forest with unaffected, alive stand, *CLRC* clearcut, *SDSF* forest with standing dead spruce, *UCFR* uncut forest (control)

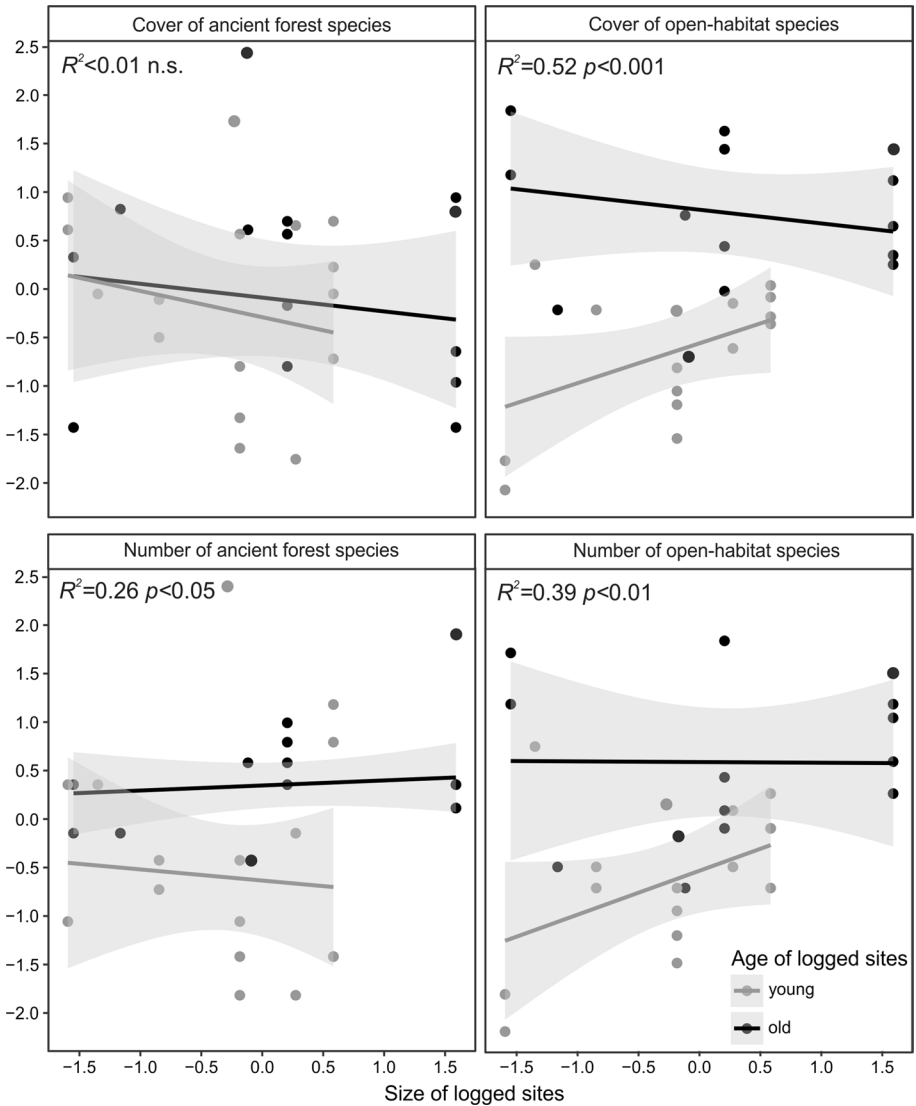


Fig. 5 Relationships between size of the logged sites and the number and cover of open-habitat species and ancient woodland indicator species depending on age of logged sites. Grey backgrounds shows standard deviations. Note scaling, centering and Yeo-Johnson transformations of the data

overrepresentation of spruce, since they were significantly more frequent and/or more abundant in their herb layer than on sites with a logged and an unlogged stand. Four species: *Acer platanoides*, *Anemone nemorosa*, *Cardamine bulbifera* and *Galium odoratum* were classified as avoiding clear-felled sites, since they occurred with distinctively lower frequencies and/or abundances there than in the other site types. In contrast, the group which revealed a preference for logged sites, with significantly higher frequency and/or abundance there compared to both other site types, included 14 species: *Agrostis*

gigantea, *Carex leporina*, *Cerastium fontanum* subsp. *vulgare*, *Juncus tenuis*, *Moehringia trinervia*, *Myosoton aquaticum*, *Ochlopoa annua*, *Poa trivialis*, *Persicaria hydro-piper*, *Rubus caesius*, *Stellaria media*, *Stellaria palustris*, *Veronica chamaedrys*, and *Veronica officinalis*.

The number of ancient woodland indicator species decreased significantly with increasing size of young logged sites ($R^2=0.26$, $p=0.006$; Fig. 5). In contrast, both the number and cover of species typically occurring in open habitats increased significantly with increasing size of young logged sites ($R^2=0.38$, $p=0.002$; $R^2=0.52$, $p<0.001$, respectively). No significant relationship with the size of logged sites was found either for young and old logged sites in the case of cover of ancient woodland indicator species, or for old clearings while analyzing the number and cover of open-habitat species, and the number of ancient woodland indicators.

Discussion

Significant differences in species composition between logged sites versus unlogged and control forests clearly indicated that logging and tree planting contributed to an increase in the number and cover of herb layer species associated with open habitats, often related to soil disturbance, whereas late-successional species of forest interiors were negatively affected. These trends were strictly associated with modified environmental conditions, especially light (Figs. 3, 4; Table 2). In this respect our findings are in accordance with those reported by Collins and Pickett (1988a), Hannerz and Hånell (1997), Roberts and Zhu (2002), Mayer et al. (2004), and Moola and Vasseur (2008). Surveys by Boch et al. (2013) also showed that, although disturbance created by forest management leads to an increase in the total species richness, this measure is not a good indicator of the conservation status of forests since it rather indicates disturbance.

At such an early stage of herb layer post-felling recovery that we studied (short time-span since clearcutting) some forest perennials were sensitive to clear-felling (sensu Ruben et al. 1999), i.e. they showed significant decrease in frequency and/or cover on logged sites compared to control and unlogged ones. This can be explained by their immediate mortality in response to mechanical disturbance and soil turnover on clear-felled sites. According to Waldron et al. (2014), the survival and persistence of forest herbs on clear-felled sites is limited when soil disturbance is high, whereas the studies by Collins and Pickett (1988a) show that lack of soil turnover does not eliminate them. Our list of species sensitive to clear-felling included *Anemone nemorosa*, *Cardamine bulbifera*, *Galium odoratum* and the juvenile individuals of *Acer platanoides*. *A. platanoides* is considered intermediate in shade tolerance (shade-tolerant when young), and it finds optimal conditions for growth on moist soils whereas it is sensitive to excessive heat (Nowak and Rowntree 1990), which explains its sensitivity to clear-felling. All other species listed are ancient woodland indicators, both in Poland (Dzwonko and Loster 2001) and Europe (Hermy et al. 1999). Such trends are consistent with the findings of Hannerz and Hånell (1997), who reported a significant decline of many ancient woodland species in reaction to clear-felling in Norway spruce forests in Sweden. Similarly, Moola and Vasseur (2008) found that many old-growth species were eliminated or declined in abundance in stands recovering after logging. Most of these sensitive taxa shared many common traits which made them vulnerable to disturbance, such as low stature, limited dispersal capacity or dependence on decaying logs. In particular, vernal geophytes were mentioned to be very sensitive to clear-felling, which is

consistent with our findings, as our list includes *Anemone nemorosa* and *Cardamine bulbifera*. Contrary to records by Collins and Pickett (1988a, b) who conducted their survey in canopy gaps, and Reader and Bricker (1992), Valladares and Ninemets (2008), we did not observe positive demographic responses, i.e. increase in abundance of shade-tolerant forest herbs with an excessive amount of light reaching the forest floor after clear-felling. Some other ancient woodland indicators, i.e. *Lilium martagon*, *Melittis melissophyllum* and *Sanicula europaea*, were less frequent and abundant in sites with a high share of spruce in the stand in both logged and unlogged site compared to control forests. It may indicate that they were negatively affected by spruce planting. All the above-mentioned herbaceous species have a transient seed bank type (Thompson et al. 1997) and are dispersal-limited (Dzwonko and Loster 2001), which poses a great risk for their chances of persistence after clearcutting and associated soil disturbance.

Our study shows that clear-felling led to an increase in the total species richness and diversity. However, it was mainly due to shade-intolerant species, typical to open habitats, which colonized sites disturbed by logging activities. Under tree canopy cover, they were either absent or observed with low frequency and cover. These observations are in accordance with the reports by Lang et al. (2009) and review by Thorn et al. (2018). Vanha-Majamaa et al. (2017) observed that the peak of the species richness took place 3 years after clear-cutting, whereas 7 years later it came to the pre-disturbance level. These findings are partly supported by our results, since, despite the shorter time gradient, we detected the most rapid changes in frequency and cover of open-habitat species on younger logged sites, which was assisted by a reduced number of shade-tolerant forest species (Fig. 5).

One of the great hazards related to salvage logging is an excessive spread of some early-successional, shade-intolerant species, especially disturbance-indicators (Boch et al. 2013; Jonášová and Prach 2008; Kurulok and Macdonald 2007; Lang et al. 2009; Lindenmayer and Noss 2006). Such dependence upon forest management was also reported from Białowieża Forest by Abs et al. (1999), who detected higher proportions of disturbance indicators (e.g. *Poa trivialis*, *Juncus effusus*, *Agrostis capillaris*), both in the herb layer and in the seed bank of the managed forests compared to strictly protected areas. This is consistent with our observations since we found significantly higher frequency and abundance of *Agrostis gigantea*, *Juncus tenuis*, *Persicaria hydropiper* and *Poa trivialis* on logged sites compared to forests where logging was not implemented. The proportion of disturbance-indicator species increases due to mechanic soil turnover, which, together with increased illumination, promotes their germination from the seed bank propagules and vegetative colonization (Collins and Pickett 1988a; Jankowska-Błaszczuk and Daws 2007; Mayer et al. 2004; Roberts and Zhu 2002). This was a probable reason for the expansion of *Rubus caesius* and *Urtica dioica* on logged sites, facilitated by increased light intensity.

As reported by Kelemen et al. (2012), all the previously mentioned tendencies take place on big clear-felled areas, whereas small gaps with a diameter not exceeding half the height of canopy trees remain relatively free of weeds, and therefore promote natural regeneration of trees and faster growth of forest perennials. In contrast to small canopy gaps, according to Cooper-Ellis et al. (1999), shrubs and grasses appearing in reaction to excessive light and space available for colonization can be regarded as persistent on big clear-felled areas. Thus, in order to avoid their expansion and consequent inhibition of the forest species recovery process, fast reestablishment of the forest canopy, providing shady conditions and suppressing further germination of disturbance indicators, is desired. This, in turn, according to Lang et al. (2009) and Thorn et al. (2018), may be achieved without logging and planting, in forests with the dead stand retained in situ. In such cases, trunks of fallen trees contribute to increased microtopographic heterogeneity, which in turn helps the

regeneration of trees and forest perennials to progress faster than on replanted clear-felled sites (Donato et al. 2006; Fraser et al. 2004; Greene et al. 2006). In addition, on clear-felled sites seedlings are prone to herbivory, whereas, in unlogged forest, decaying logs act as a physical barrier, blocking access to herbivores and creating conditions of a landscape of fear, avoided by herbivores because of the frequent hunting activity of large predators (Kuijper et al. 2014; Smit et al. 2015). On the other hand, salvage logging leads to homogenization of environmental conditions (Waldron et al. 2014), which in turn reduces the capacity of forest perennials to establish, since it modifies light and humidity conditions (Lang et al. 2009). Thus, active restoration of tree cover by planting hampers natural regeneration processes and reduces the diversity of slow-recovering species (Lindenmayer and Noss 2006; Thorn et al. 2017).

The time-span of vegetation changes in our study was too short to provide data on the length of the period needed for recovery of forest species affected by logging. However, some surveys indicate that many species sensitive to clear-felling recover within a few decades after stand reestablishment, and the logging effect may substantially diminish over approximately 25 years (Ruben et al. 1999). However, full regeneration of the herbaceous layer can take longer than 60 years from clearcutting (Ruben et al. 1999). Collins and Pickett (1988a) claim that, even in 70-years-old stands, herb species populations may still be changing in reaction to former logging. In other studies cited by Roberts and Zhu (2002) the recovery time was estimated as 50 to 80 years (in the latter case the time of recovery was longer than the implemented logging cycle). In some cases, it seems that pre-disturbance herb layer assemblages may never fully recover, especially when the time needed for restoration is not allowed because of the short stand rotation cycle. Bearing these results in mind, one can expect that, in the case of the studied sites, the pre-felling population dynamics of many herb layer perennials might already not have been in full equilibrium, as a legacy of forest management practices implemented there 50–90 years ago, when the currently felled spruce stands were planted. This may be especially true when taking into account the high capacity of spruce to modify environmental conditions for other species: decreased light, increased humidity (Białobok 1977), decreased pH, and increased C stocks of soil (Dawud et al. 2016). Thus, we can expect successive, additional, negative effects of these disturbances on the forest herbs' future demographic changes. These trends will presumably be coupled with a risk of the appearance of disturbance indicators, germinating from the soil, since, according to Brown and Oosterhuis (1981) and Honnay et al. (2002), most of them are species with long-term persistent seed banks. In the presence of disturbance, such species appear abundantly from the soil seed bank because they are photoblastic, and require a high red:far-red (R:FR) ratio of light for germination (Jankowska-Błaszczuk and Daws 2007), which is provided in natural forest gaps and in clearcuts. One should stress that despite a few decades of growth of spruce on sites formerly occupied by oak-hornbeam forests the number of shade-tolerant forest species is still high in disturbed, unlogged forest compared to logged sites. It is an indication that there is a good prospect that such forests transformed by former management will recover their herb layer once their stand is left unlogged after the outbreak.

Recovery of the herb layer composition on clear-felled areas takes place via two simultaneous processes, i.e. vegetative resprouting via root suckers, rhizomes, stolons and buds of the plant populations which survived the disturbance (Blair et al. 2016; Lindenmayer and Ough 2006), and via germination from viable seeds. Seeders on the clearcuts germinate either from the local seed bank (germination is enhanced by increased light access and soil disturbance during logging and planting operations) or from the seed rains (Mayer et al. 2004). Similarly, vegetative spread is possible from the local re-growth and from

neighbouring forests. Thus, as well as the regeneration in situ, herb layer recovery is possible as a result of recolonization from the nearby populations of forest species existing in the adjacent, unfelled forest stands (Mayer et al. 2004). Apart from wind-dispersed species, the migration of most forest perennials from outside is much slower than regrowth from the populations which survived in situ (Mayer et al. 2004), since most ancient forest species rely on vegetative rather than generative spread and their seeds have low migration capacities (Hermy et al. 1999). Thus, the chance of recovery of the herb layer from the local populations in naturally disturbed forests increases if their level of disturbance is not artificially increased by logging and planting of trees (Lindenmayer et al. 2017). Otherwise, as in the case of many species in our study, their cover on logged sites substantially decreases in comparison to control and unlogged stands, because logging leads to mortality of herbaceous species and to alterations of habitat conditions, promoting light-demanding, competitive species, such as *Rubus caesius*. Jonášová and Prach (2008) noticed that the negative effects of salvage logging on vegetation are greater than those of the insect outbreak itself, which was corroborated by our results. Since salvage harvesting is not consistent with the conservation priorities, it should not be permitted in protected areas (Jonášová and Prach 2008; Thorn et al. 2018). This should also refer to “Białowieża Forest” World Heritage Site, where protection of ecological and biological processes and biological diversity should be a priority (Kujawa et al. 2016; Mikusiński et al. 2018). Despite many legacies of forest management observed in the managed stands of BF (Bobiec 1998), similarly to Abs et al. (1999), we state that these forests still have great potential to recover after former human-induced disturbance owing to the general low level of forest transformation and existing patches of forest of natural origin scattered in the matrix of younger, managed stands. However, if salvage logging continues and mature forests are successively felled, these refuges of naturalness and sources of rich populations of forest species will eventually disappear. A recent study by Mikusiński et al. (2018) shows how serious and detrimental to the integrity of this forest complex the logging was that took place in 2017 and 2018. According to these authors, in 2018 the total area of clear-felled sites in BF amounted to 675 ha, including 229 ha in old-growth stands, which resulted in a 26% increase in fragmentation of this forest complex.

Conclusions

Our results demonstrate that enriched biodiversity observed on salvage-logged sites in the initial stages of their vegetation recovery does not contribute to the enhanced value of BF. Actually, the effect is the opposite, since salvage logging breaks the natural ecological processes of forest dynamics and facilitates colonization of forest ecosystems by light-demanding, competitive species, associated with disturbed forest sites but hinders the number and cover of late-successional, shade-tolerant forest species. In order to retain and, where needed, restore the high conservation value of BF, salvage logging and tree planting in this forest complex should be stopped.

We proved that spruce-dominated forests growing on the habitats of mixed deciduous forests, currently affected by bark beetle infestation, revealed great potential for natural recovery of understory species typical to their original *Tilio-Carpinetum* forest habitat. Thus, from the conservation point of view, post-disturbance logging is not needed for the successful regeneration of the herb layer. Furthermore, Paluch (2002) and Miścicki

(2016) claim that in BF we are witnessing the steady transformation of the subboreal forest communities dominated by Norway spruce towards the mid-European broadleaved forests. Consequently, in the face of global climate change, the best scenario for forest stands affected by bark beetle is to allow spontaneous recovery towards the mixed broadleaved forest.

Acknowledgements We would like to express our gratitude to Natalia Bojarowska, Maciej Psych Smykowski (Greenpeace Polska) and Tomasz Zdrojewski (Dzika Polska) for their help in finding the clear-felled sites' localities and measuring their size. Anna Orczewska expresses her gratitude to Dr. Sylwia Wierzycholska for hosting her in Białowieża during the field work.

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Affiliations

Anna Orczewska¹  · Patryk Czortek² · Bogdan Jaroszewicz²

✉ Anna Orczewska
anna.orczewska@us.edu.pl

¹ Department of Ecology, Faculty of Biology and Environmental Protection, University of Silesia, Bankowa 9, 40-007 Katowice, Poland

² Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Sportowa 19, 17-230 Białowieża, Poland