Evaluation of Early Stage Regeneration of Forest Communities Following Natural and Human-caused Disturbances in the Transitional Zone between Temperate and Hemiboreal Forests

VYTAUTAS SUCHOCKAS [1,2], ALFAS PLIŪRA [1,2], JUOZAS LABOKAS[3], VAIDOTAS LYGIS[3,4], DOROTA DOBROWOLSKA[5], JURGA JANKAUSKIENĖ [3] AND RITA VERBYLAITĖ[1]

[1] *Institute of Forestry, Lithuanian Research Centre for Agriculture and Forestry, Liepų str. 1, LT-53101 Girionys, Kaunas reg. (Lithuania); * v.suchockas@mi.lt*

[2] *Aleksandras Stulginskis University, Studentų str. 13, LT-53361 Akademija - Kaunas (Lithuania)*

[3] *Institute of Botany of Nature Research Centre, Akademijos str. 2, LT-08412 Vilnius (Lithuania)*

[4] *Kaunas Forestry and Environmental Engineering University of Applied Sciences, Liepų str. 1, LT-53101 Girionys, Kaunas reg. (Lithuania)*

[5] *Forest Research Institute IBL, Braci Leśnej 3, PL-05-090 Raszyn (Poland)*

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Abstract

Increasing occurrence of natural and human-caused disturbances threatens sustainability of forest ecosystems, their ability to regenerate and maintain biological diversity. Simultaneously, forest tree species penetrate into abandoned agricultural lands, the areas of which have noticeably increased during the last decades. The aim of this study was to evaluate and compare the development of regenerating forest tree communities in terms of their growth, competition and species composition in ecosystems affected by various environmental stressors such as windthrows, insect pests, fungal diseases, traditional clearcuttings and agricultural land-use legacy. Lithuania, being located in the transition between the boreal and continental biogeographical regions of Europe, has been considered a favourable research area as both conifer and broadleaved tree stands as well as mixed ones are common here. Research methods used included inventory of vegetation and assessment of quantitative characteristics and sanitary condition of six regenerating forest tree species – Scots pine, Norway spruce, silver birch, pedunculate oak, common ash and black alder – in 7–8 circular research plots (50.24 m^2 each) per study site with total 17 study sites. Results of the study demonstrated that forest regeneration takes place in all disturbed ecosystems, although high variation in space and time was present. Species composition of the regenerating forest ecosystems depends on those prevailing before disturbance, although, pioneer species out-compete the others. The most intensive forest regeneration takes place in those forest ecosystems which were subjected to direct human impact, i.e., clear cuttings, and less intensive regeneration, particularly, that with the target species, takes place on sites cleared of windthrows and where sanitary fellings were applied. Although non-target species depending on habitat type usually prevail on cutting sites, numbers of saplings of target species are sufficient for the regeneration of high productivity forest ecosystems and development of the new ones given the competing species will be controlled by silvicultural measures. The pioneer herbaceous species established on areas affected by disturbances affect regeneration and species composition of the future forest communities.

Keywords: ecosystem disturbance; regeneration; abandoned agricultural lands; clearcutting; sanitary fellings; windthrows.

Introduction

Numerous studies report that an increased scale and frequency of abiotic and biotic disturbances (often related to climate change) threatens sustainability of forest ecosystems, their ability to regenerate, to maintain biological diversity and ecological successions typical for hemiboreal forests (Hobbs and Huenneke 1996, Dale and Haeuber 2001, Mitchell 2013, etc.). The condition and structure of forest ecosystems depend on temporal and spatial patterns of both management interventions and natural disturbances. It has been found that spatial characteristics of disturbances affect succession rates of plant communities and regeneration after suffered damages (Runkle 1985, Jørgensen and Müller 2000, Jensen and Bourgeron 2001). Disturbances also affect ecosystem productivity during changes of elements in ecosystem composition, their cycles in time and space, amounts of biomass, rates of community development as well as ratios between live and dead biomass (Dale and Haeuber 2001, Lindenmayer, McCarthy 2002). Natural disturbances occur in all forest ecosystems being an indispensable driver of renewal and regeneration, maintaining diversity and changes in natural ecosystems (Pickett and White 1985, Aber and Melillo 1991, Holling 1992, Attiwill 1994, Bengtsson et al. 2000).

According to Everham and Brokaw (1996), regeneration of an ecosystem after catastrophic disturbances (windthrows) may proceed following one of the four paths: regrowth (sprouting of surviving trees), recruitment (establishment of seedlings of early successional species), release (rapid growth of suppressed subcanopy trees and seedlings) and repression (invasion of herbaceous vegetation that restrict the regrowth or recruitment of trees). Which of these ways is followed depends on a variety of environmental factors? Each ecosystem has its own individual 'memory', which shapes the primers of a new, regenerating ecosystem. The ecosystem memory is comprised of its remainders and new derivatives, or substances, shaped up after a natural disturbance (Peterson 2002, Schaefer 2009, Johnstone 2016). Although natural disturbances frequently create favourable conditions for formation of tree communities different from those that were present in a former stand, the newly formed communities usually inherit features of former stands with admixtures of new components depending on the character of natural disturbance. However, temporary plant communities without trees may also develop. Even frequently occurring and severe natural disturbances rarely eliminate all the elements of a former stand: in most cases, at least single seed-bearing trees, undergrowth or both survive (Foster et al. 1998, Franklin et al. 2000, 2002). If there is a sufficient amount of undergrowth before the natural disturbance occurs, a new tree community in the disturbed ecosystem readily regenerates (Henderson et al. 1989).

There are two hypotheses about prevalence of species following natural disturbances: one of them states that if a tree dies in the consequence of a natural disturbance, its place is occupied by shade-tolerant tree species which already grew in that place before the opening emerged (Egler 1954, Mueller-Dembois and Ellenberg 1974, Spurr and Barnes 1980). Another hypothesis states that new species settle down in openings created following a natural disturbance. Seedlings of highly competitive species occupy open spaces and may compete with every later-emerged individual. Dobrowolska (2006) noted that in openings following natural disturbances and in natural forest glades, species composition in a stand renews and new arrivals form a backbone of the future stand composition are formed. It should be noted also that disturbances may also increase a probability of invasive species to settle down (Mitchell et al. 2002).

Natural disturbances play an important role in controlling composition of ecosystem elements and, at the same time, biological diversity. Under the impact of frequent and catastrophic disturbances, diversity of tree species may be sustained at an average level (diversity will change little). Species diversity increases in stands if they are subjected to natural disturbances of medium strength as estimated by their intensity and frequency, and which do not destroy ecosystem, leaving a sufficient time span for ecosystem regeneration between the disturbances (e.g. Petraitis et al. 1989). Meanwhile, in ecosystems affected by disturbances of low intensity the species diversity will increase in openings or in undisturbed areas and diversity will increase along with the time span between severe large-scale (catastrophic) disturbances. Natural disturbances may reduce species diversity when poorly-adaptable species prevail prior to disturbance, or when the disturbance destroys the ecosystem before it is ready for regeneration (immature stand, no seed-bearing individuals available).

In Lithuania, being located in the transitional zone between the temperate and hemiboreal forests, the most common natural abiotic disturbances are windthrows and windsnaps; yet extreme snowfall, local floods, droughhts, and considerable fluctuations of water table level may also cause serious damages to forests. Meanwhile, forest fires usually occur due to human causes. The most frequent natural biotic disturbances include damages caused by insects, fungal diseases, wild game, and establishment of invasive plant species. Modelling of likely climate change effect on forest ecosystems (Ozolinčius et al. 2014) suggests that growth conditions for most of the deciduous tree species in Lithuania will improve because of increasing mean air temperature, CO_2 concentration and amounts of precipitation. At the same time, following climate warming, native coniferous species (Norway spruce, Scots pine) may suffer increasingly, and their distribution range may shift northwards.

With this regard it becomes also essential to estimate the possibilities for new forest ecosystems to emerge on abandoned agricultural lands the areas of which has significantly increased since 1990s. Based on satellite data, an area of 6.4 million km^2 across Central and Eastern Europe and the Balkan Peninsula is considered abandoned farmland (Alcantara et al. 2013). The total area of abandoned lands in Lithuania currently amounts to 64.174 thousand ha (Nacionalinė Žemės Tarnyba 2017).

The knowledge on impact of disturbances on dynamics of disturbed forest ecosystems is necessary to safeguard ecosystem functioning, forest regeneration and biodiversity. Despite increasing attention by the international researcher community on the matter, up to now little information is available on how different tree species, communities and populations adapt to the changing environment; which species have best developed mechanisms to cope with stress-induced damages. In addition, there is a lack of knowledge on how ecological response and phenotypic plasticity can help species to adapt to ever changing and often stressful environmental conditions. Currently increasing attention is being drawn to the development of forest management systems based on imitation of natural processes and to investigations into tree tolerance to natural disturbances. As natural disturbances will likely increase in scale and range along with climate change and likely increased demand for wood in the near future, it is urgent to focus further studies on safeguarding of the precious resources of forest ecosystem by all possible ways.

The main aim of the presented study was therefore to evaluate and compare development of regenerating forest tree communities in forest ecosystems affected by various environmental stressors like windthrows, traditional clearcuttings, sanitary fellings in areas affected by infectious diseases and insect pests, or in newly formed ecosystems on abandoned agricultural land, where economically important tree species, such as Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.), silver birch (*Betula pendula* Roth), pedunculate oak (*Quercus robur* L.), common ash (*Fraxinus excelsior* L.) and/or black alder (*Alnus glutinosa* (L.) Gaertn.), were dominant components prior to a certain disturbance or have emerged after disturbance/change in land-use legacy, with respect to their growth and competitive abilities.

Materials and Methods

Study sites

Lithuania, being located in the transition between the boreal and continental biogeographical regions of Europe (EEA 2002), has been considered as a favourable research area as both conifer and broadleaved tree stands as well as mixed ones are common here and this transitional zone is expected to shift northwards in the course of climate change. Naturally regenerating forest tree communities were selected in sites affected by four types of disturbances including change of land-use legacy: a) cleared windthrow sites (Scots pine stands: 2 sites, and Norway spruce stands: 2 sites); b) sites subjected to traditional clearcuttings (Norway spruce stands: 2 sites, Scots pine stands: 1 site, black alder stands: 1 site, and stands of black alder admixed with silver birch: 1 site); c) stands affected by an infectious disease (common ash stands infected by *Hymenoscyphus fraxineus* Baral et al.: 3 sites) and insect pests (pedunculate oak stands: 2 sites) and thus subjected to sanitary fellings; and d) abandoned agricultural lands (emerging Scots pine stands and silver birch stands: 2 sites) (Table 1). Each study site covered an area from 3 to 7 ha.

Inventory of study sites

Inventory of vegetation (trees, shrubs and herbaceous plants) and assessment of quantitative characteristics and sanitary condition of six regenerating forest tree species (hereafter referred to as *target species*), such as Scots pine, Norway spruce, silver birch, pedunculate oak, common ash and black alder, were carried out in disturbed areas (hereafter referred to as *study sites*) listed in Table 1. Circular research plots with a radius of 4 m (plot area = 50.24 m^2) were used for inventory at each study site. The first research plot within a study site was set at a random location but not closer than 15 m from the border of that study site. All the rest of the plots (7-8 per study site) were distributed with intervals of 20–25 m along a transect stretching at a random direction across each study site. At each plot, a complete record of all trees of the regenerating target species (Table 1) was performed, including measurement of their height above ground with an accuracy of 1 cm, and visual evaluation of sanitary condition. The number of trees found in a plot was recalculated to a per hectare basis. Seedlings were defined as trees less than the height of 1.3 m, and saplings were defined as trees of 1.3 to 5 m height. In general, they are called regeneration.

In every research plot, the forest site types of former (original) and new (regenerating) forest were identified according to Karazija (1988). A phytosociological description was made in each research plot, and significance of each species was determined according to its abundance and cover percentage. The following floristic-phytosociological characteristics were determined: species diversity, frequency of occurrence (%) and relative abundance (%). Also, composition and percent coverage of dominant species of underbrush and herbaceous species were determined in each plot. As a reference for Latin names of species, an online checklist (The Plant List 2013) was consulted.

In each research plot, distance from each tree of target species to a closest seed tree of the respective species was recorded with the reference to four cardinal directions. Spatial irregularity of forest regeneration was evaluated using variation coefficient of mean number of seedlings/sprouts of all regenerating tree species and, separately, only of the target tree species. Structure of forest regeneration was evaluated by regularity of spatial distribution of trees around the reference point (*Winkelmass* index, W_i), by species composition (*mingling* index, M_i) and by differentia-

Table 1. Main characteristics of study sites selected in areas affected by four types of disturbances

Study site	Type of disturbance / change in land-use legacy	Species composition prior to disturbance (% of stem volume) /(Age)/ Stocking level	Coverage of dominated herb species prior to disturbance %	Regenerating target tree species	Forest site type[a]	Latitude N Longitude E	Seed source (origin of seedlings)	Activities after the disturbance
EVK1Dub	Windthrow in 2012, completely destroyed stand	100 spruce /(50)/ 0.9	*Oxalis* 55 *Fragaria* 15 *Vaccinium* 30	silver birch, Scots pine	*Oxalidosa*	54° 49.585' 23° 59.990'	Adjacent stands (newly emerged seedlings)	Timber extraction
EVK2Dub	Windthrow in 2012, completely destroyed stand	80 spruce / (65)/0.7 10 pine 10 oak	*Vaccinium* 60 *Oxalis* 20 *Luzula* 20	Norway spruce	*Myrtillo-oxalidosa*	54° 50.150' 24° 04.109'	Adjacent stands (newly emerged seedlings)	Without felling
PVK14Pri	Windthrow in 2012, completely destroyed stand	100 pine / (75)/0.7	*Vaccinium* 90 *Pleurosium* 5 *Hylocomium* 5	Scots pine. silver birch	*Vaccinio-myrtillosa*	54° 39.915' 24° 05.506'	Adjacent stands (newly emerged seedlings)	Timber extraction
PVK18Dub	Windthrow in 2012. completely destroyed stand	60 pine / (70)/0.8 20 spruce 20 birch	*Oxalis* 55 *Fragaria* 20 *Aegopodium* 25	silver birch	*Oxalido-nemorosa*	54° 49.267' 24° 01.087'	Adjacent stands (newly emerged seedlings)	Timber extraction
JK5Any	Clearcuting in 2013. completely cut off stand	50 alder / 0.4(80)/0.7 40 birch 10 spruce	*Carex* 80 *Sphagnum* 20	black alder. silver birch	*Myrtillo-sphagnosa*	55° 41.132' 25° 07.591'	Seedtree (newly emerged seedlings)	Timber extraction
EK13Tyt	Clearcuting in 2013. completely cut off stand	50 spruce /(103)/0.7 40 pine 10 birch	*Oxalis* 65 *Fragaria* 15 *Vaccinium* 20	Norway spruce. silver birch	*Oxalidosa*	55° 32.846' 23° 09.874'	Adjacent stands (newly emerged seedlings)	Timber extraction
PK6Any	Clearcuting in 2013. completely cut off stand	80 pine / (100)/0.6 20 spruce	*Vaccinium* 75 *Pleurosium* 15 *Hylocomium* 10	silver birch. Scots pine	*Vaccinio-myrtillosa*	55° 40.519' 25° 06.700'	Adjacent stands (newly emerged seedlings)	Timber extraction
JK15Pri	Clearcuting in 2013. completely cut off stand	70 alder / (70)/0.8 10 aspen 10 birch 10 spruce	*Oxalis* 55 *Rubus* 10 *Luzula* 35	black alder. common ash	*Oxalido-nemorosa*	54° 43.950' 23° 53.750'	Seedtree (newly emerged seedlings)	Timber extraction
EK17Dub	Clearcuting in 2013. completely cut off stand	80 spruce / (80)/0.7 20 pine	*Vaccinium* 80 *Oxalis* 10 *Luzula* 10	silver birch. Norway spruce	*Myrtillo-oxalidosa*	54° 48.318' 24° 04.609'	Adjacent stands (newly emerged seedlings and undergrowth)	Timber extraction
PK21Dub	Clearcuting in 2013. completely cut off stand	70 pine / (80)/0.8 30 spruce	*Vaccinium* 80 *Oxalis* 10 *Calamagrostis* 10	silver birch. Scots pine	*Myrtillo-oxalidosa*	54° 50.022' 24° 09.628'	Adjacent stands (newly emerged seedlings)	Timber extraction
ASK8Jon	Sanitary felling in 2013. completely cut off stand	50 oak / (130)/0.4 20 ash 20 spruce 10 birch	*Oxalis* 75 *Aegopodium* 10 *Luzula* 15	pedunculate oak. common ash	*Oxalido-nemorosa*	55° 09.175' 24° 06.967'	Seedtree (newly emerged seedlings and undergrowth)	Timber extraction
ASK10Ked	Sanitary felling in 2013. completely cut off stand	40 oak / (130)/0.4 40 ash 10 spruce 10 birch	*Oxalis* 75 *Hepatica* 25	common ash. silver birch. pedunculate oak	*Oxalido-nemorosa*	55° 13.473' 23° 56.689'	Seedtree (newly emerged seedlings)	Timber extraction
USK16Ked	Selective sanitary fellings in 2013	50 ash / (60)/0.4 20 alder 20 birch 10 oak	*Geum* 35 *Deshampsia* 30 *Filipendula* 25	common ash	*Carico-mixtoherbosa*	55° 13.567' 23° 58.271'	Shelter wood (newly emerged seedlings)	Timber extraction
USK19Ukm	Sanitary felling in 2013. completely cut off stand	70 ash / (70)/0.6 30 alder	*Ranunkulus* 65 *Geum* 20 *Carex* 15	common ash. grey alder	*Carico-mixtoherbosa*	55° 16.191' 24° 40.561'	Seedtree (newly emerged seedlings)	Timber extraction
USK20Kur	Selective sanitary fellings in 2013	60 ash / (70)/0.8 40 spruce	*Geum* 40 *Calamagrostis* 35 *Carex* 25	common ash	*Carico-mixtoherbosa*	56° 00.131' 22° 47.403'	Shelter wood	Timber extraction
BZU7Any	Abandoned agricultural land since 2013	No tree cover	Agricultural plants	silver birch	*Oxalidosa*	55° 38.331' 24° 46.245'	Adjacent stands (newly emerged seedlings)	Suspended agricultural activity since 2013
BZU12Tyt	Abandoned agricultural land since 2013	No tree cover	Agricultural plants	silver birch. Scots pine	*Vaccinio-myrtillosa*	55° 31.934' 23° 10.858'	Adjacent stands (newly emerged seedlings)	Suspended agricultural activity since 2013

[a] according to Karazija (1988). based on key herb species

tion-domination (*domination* index, U_i) (Gadow and Hui 2002). Determination of *Winkelmass* index, W_i, is based on considering angles between the neighbouring trees (Gadow 1993). The value of W_i varies from 0, in the case of regular distribution, when angles between neighbouring trees are close to right (90°), to 1, in the case of irregular distribution, when angles between neighbouring trees are acute (<90°) on one side and exceeding 270° on the other side (Hui et al. 1998). If $W_i \le 0.5$, it indicates regular, at $0.5 < W_i \le 0.6$ it reflects random, and if $W_i > 0.6$, it represents group distribution of trees (Pommerening 2002, Szmyt 2012, Szmyt, Korzeniewicz 2014).

Mingling index, M_i, is an ecological standard measure for species diversity and it describes the degree of mixing of tree species in a stand (Gadow 1993). Index M_i varies from 0, when all neighbours of the reference tree belong to the same species (low species diversity) to 1, when all neighbours belong to different species than the reference tree (high species diversity). Low M_i values indicate that homogeneous groups of one tree species prevail in a stand, while high M_i values show that the stand is composed of a high variety of more or less evenly distributed tree species.

Stem height was used as a main parameter to describe growth rates of regenerating trees and to assess their differentiation and competitiveness in a newly formed forest ecosystem. Height differentiation of trees was evaluated using index of domination, U_i, which is determined by evaluating height differences between the neighbouring trees and the reference one (Hui et al. 1998). Index U_i varies from 0, when all neighbours are lower than the reference tree (low differentiation of heights), to 1, when all neighbours are taller than the reference tree (high differentiation of heights).

Shannon's and Simpson's diversity indices (Beals et al. 1999, 2000) and Pielou's evenness indices (Pielou 1966) were computed both including all plant species within a research plot and including tree species only.

Point intercept method (Bonham 2013) was employed to assess ground vegetation cover (including small shrubs) for each plot. A metal sampling pin (4 mm in diameter and 120 cm length) was used to place at the intervals of 50 cm along two line transects, perpendicular to each other and pointing each at N–S and E–W directions across the circular plot. Total 32 points were sampled per plot area. Percent cover was calculated by dividing the number of hits on plant species by the total number of hits.

Statistical analysis

To test the significance of impact of disturbance type and site on regeneration characteristics, the two-way variance analysis of data was done using MIXED procedure in SAS (SAS® Analytics Pro software suite, versions 12.1 and 9.3, 2016) which is based on the mixed model equations (MME) and restricted maximum likelihood (REML) method. The significance of effects was tested using an *F*-test. The following linear model was used:

$$Y_{ikl} = \mu + D_k + S_{l(k)} + e_{ikl}, \quad (1)$$

where: Y_{ikl} is an observation on i^{th} sub-plot from in l^{th} site in k^{th} disturbance type, *m* is the overall mean, D_k is the effect due to the k^{th} disturbance type, $S_{l(k)}$ is the effect of l^{th} site in k^{th} disturbance type, e_{ikl} is the random residuals. The models assume that all effects are fixed.

To evaluate significance of differences between different study sites and between disturbace types Student's *t*-test for independent samples was performed using options 'lsmeans', 'cl', and 'dif' of the SAS procedure MIXED (SAS® Analytics Pro 12.1, 9.3, 2016).

For evaluation of regeneration of each target tree species depending on various bioecological factors, the SAS procedure RSQUARE was used to construct all possible models of multiple regressions, to analyse their fitness and to select the most suitable linear combinations of factors aiming at high determination coefficient of regression, R^2, under a low-to-moderate number of factors included into an equation. The character and strength of dependence were analysed by the means of multiple regression analysis using the SAS procedure REG (SAS® Analytics Pro 12.1, 9.3, 2016). The following equation of a multiple linear regression was used:

$$Y = a + b_1{*}X_1 + b_2{*}X_2 + \ldots + b_n{*}X_n, \quad (2)$$

where: *Y* is the abundance of regeneration; *a* is the free component of the equation; $b_1, b_2, \ldots b_n$ are the coefficients of regression according to the factors studied; $X_1, X_2 \ldots X_n$ are the ecological and biological variables, as defined in Table 2.

Table 2. Ecological and biological variables analysed in multivariate regression analysis of forest regeneration abundance

Label	Variable	Unit of measurement	Label	Variable	Unit of measurement
X_1	trophotope of habitat	scores	X_{12}	cover of reed-grass	%
X_2	stocking level of former stand	scores	X_{13}	cover of heath	%
X_3	distance to seed tree	m	X_{14}	cover of wood sorrel	%
X_4	cover of tree canopies	%	X_{15}	cover of goatweed	%
X_5	cover of underbrush	%	X_{16}	cover of raspberry	%
X_6	cover of common hazel	%	X_{17}	cover of ferns	%
X_7	cover of alder buckthorn	%	X_{18}	cover of meadowsweet	%
X_8	cover of willows	%	X_{19}	cover of other herbs	%
X_9	cover of herbs (all species)	%	X_{20}	no vegetation cover	%
X_{10}	cover of red bilberry	%	X_{21}	cover of woody debris	%
X_{11}	cover of bilberry	%	X_{22}	humidity of habitat	%

For different species, only equations that included factors with reliable effects based on Student's *t*-criterion and probability values ($P<0.05$) were chosen.

To group indices of spatial pattern, species-specific and developmental evenness as well as different indices of species diversity into principal components, a factorial analysis was carried out using the SAS procedure FACTOR (SAS® Analytics Pro 12.1, 9.3, 2016). Load coefficients of individual features within each factor were determined; based on that, eco-biological sense and importance of each component was identified. In the next step, study sites were aggregated into groups based on principal components as established by factorial analysis using the FACTOR procedure and scoring with the SAS procedure SCORING (SAS® Analytics Pro 12.1, 9.3, 2016) and plotted using the SAS procedure PLOT. The dendrograms were built by performing Average Linkage Cluster Analysis with the SAS procedure TREE (SAS® Analytics Pro 12.1, 9.3, 2016).

Results

The results of the study showed that spontaneous forest regeneration takes place in all investigated ecosystems (study sites) (Figure 1).

black alder, aspen and/or Scots pine usually constituted a major component of the regenerating stand (Figure 2). In clearcuttings within Norway spruce stands, spruce regeneration was also quite abundant. Regeneration of silver birch was good on spruce sites and comprised 3–8 thous. seedlings per hectare. Another target species regenerating in clearcuttings within Norway spruce stands was Scots pine, yet its abundance did not exceed one thousand seedlings per hectare (Figure 2). Regeneration in clearcutting sites within black alder stands consisted almost exclusively of deciduous tree species. Density of black alder seedlings comprised more than 10 thous. stems per hectare (Figure 2). In a vigorously regenerating site, JK5Any, where silver birch made a large fraction in composition of black alder stand before felling it, birch regeneration was as abundant as that of black alder. In clearcutting sites within Scots pine stands, 2–4 species (birch, pine, spruce and oak) prevailed; individuals of other species were found only occassionally (Figure 2). Density of pine seedlings in both sites reached 7–10 thous. stems per hectare, yet regeneration of silver birch was more abundant (13–14 thous. stems per hectare). Mean height of the regenerating trees varied a lot depending on tree species, site characteristics and disturbance/land-use legacy type (Figure 3). On the clearcutting sites seedlings

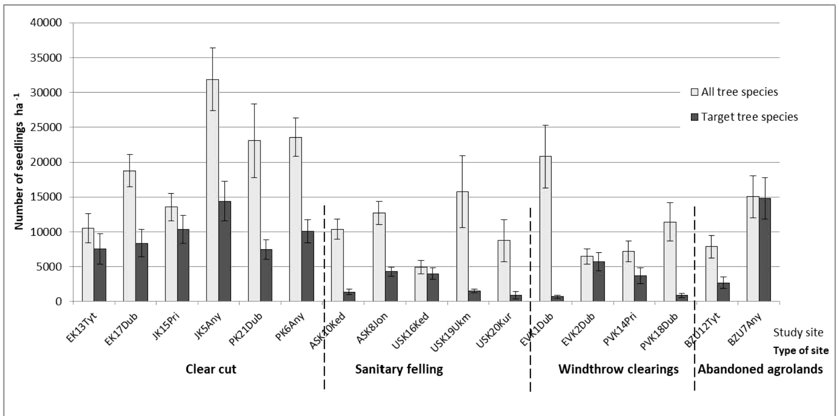

Figure 1. Mean number of regenerating seedlings in areas affected by different types of disturbances/land-use legacies (see Table 1). Bars indicate mean values and pins indicate the standard errors

Two-way ANOVA (SAS MIXED procedure) has shown that the type of disturbances and study sites had significant impact on most regeneration characteristics, except impact of type of disturbances on spatial regularity index of regeneration, *Wi,* and regeneration domination index, *Ui*, and impact of study sites on regeneration domination index, (*Ui*) (Table 3.)

In clearcutting sites, which are considered as severely disturbed ecosystems, the most intensive forest regeneration was observed (Figure 1). Although in most cases non-target tree species prevailed, the regeneration by target trees was also good and comprised 7–15 thous. seedlings per hectare (Figure 1). In areas subjected to traditional clearcuttings, 2–4 pioneer tree species such as silver birch,

Table 3. Results from mixed linear model two-way ANOVA of forest regeneration characteristics on different disturbance types and study sites: *F*-criteria and probabilities (*P*) of effects

Regeneration characteristics	Disturbance types		Study sites	
	F	*P*	*F*	*P*
Abundance of regeneration	11.84	<0.001	4.29	<0.001
Abundance of target regeneration	30.94	<0.001	4.55	<0.001
Regeneration spatial regularity index W_i	0.22	0.882	2.38	0.008
Regeneration species migling index M_i	3.92	0.011	3.54	<.0001
Regeneration domination index U_i	0.28	0.841	1.73	0.066
Shannon diversity index H	13.13	<0.001	9.16	<0.001
Pielou's evenness index J' (=Shannon evenness index E)	11.28	<0.001	6.23	<0.001
Simpson diversity index D	7.36	0.001	4.88	<0.001
Simpson evenness index E	4.91	0.003	2.07	0.022

Total degree of freedom. *DF*=102. disturbance types' *DF=3*. study sites' *DF=13* of broadleaved tree species were distinguished by their height. The most regular distribution of regenerating trees (*Wi* < 0.2) was observed in the clearcut black alder stand, JK5Any, and pine stand, PK6Any, (Figure 4). We found more than one regenerating tree species and in most study sites at least two trees neighbouring the central reference tree representing different species. The traditional clearcutting sites were represented by the lowest values of mingling index M_i (EK13Tyt), and the highest values of domination index U_i (EK17Dub) (Figure 4).

Student's *t*-test (SAS MIXED procedure) has shown that compared to traditional clearcutting sites, significantly lower ($P < 0.001$) numbers of regenerating trees were observed in areas subjected to sanitary clearfellings (Figure 1). In these sites, fast-growing broadleaves dominated, and target tree species usually comprised only a small fraction in the regeneration. An increased species diversity was observed in clearfelled stands devastated by insect pests (oak stands on *Oxalido-nemorosa* forest site type) or infectious fungal disease (ash stands on *Carico-mixtoherbosa* forest site type). Five to seven regenerating species could be found on oak sites, while on ash sites the number of species was restricted to 3–6 (Figure 2). Overall density of regenerating target trees was not high on all sites and rarely exeeded 10 thous. stems per hectare. Mean height of the regenerating trees varied a lot depending on tree species, site character-

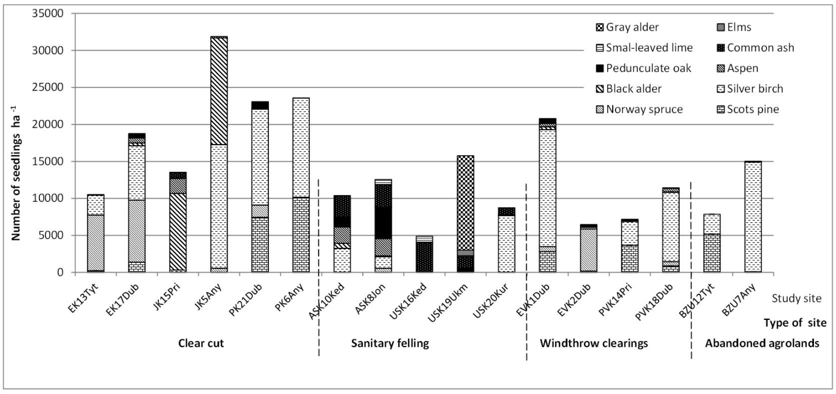

Figure 2. Proportion of mean number of regenerating seedlings in areas affected by different types of disturbances/ land-use legacies (see Table 1)

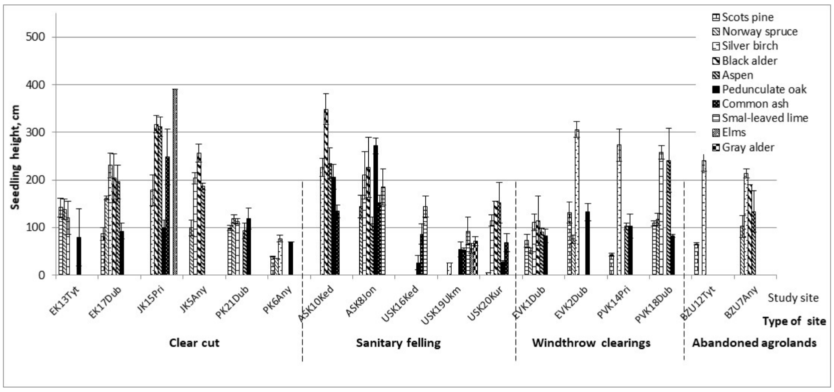

Figure 3. Mean heights of regenerating seedlings in areas affected by different types of disturbances/land-use legacies (see Table 1). Bars indicate mean values and pins indicate the standard errors

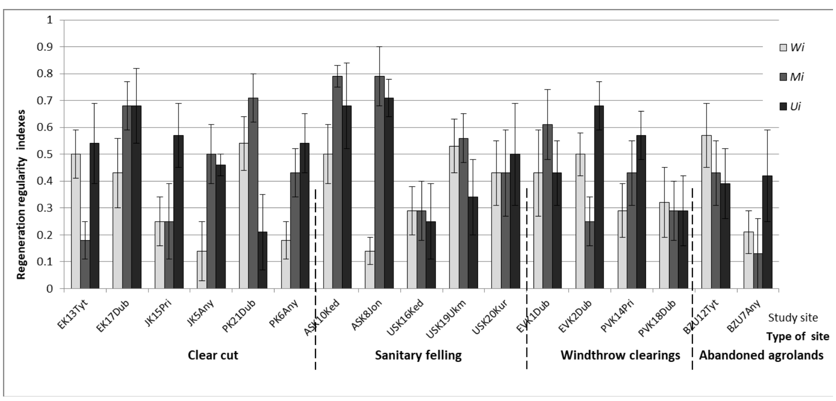

Figure 4. Forest regeneration spatial structure indices.- *Winkelmass* index (W_i). species migling index (M_i) and domination index (U_i). calculated for regenerating tree species in areas affected by different types of disturbances/land-use legacies (see Table 1). Bars indicate mean values and pins indicate the standard errors

istics and disturbance/land-use legacy type (Figure 3). On the sanitary felling sites seedlings of broadleaved tree species were distinguished by their height, as well as on the clearcutting sites. The most regular distribution of regenerating trees ($Wi < 0.2$) was observed in an oak site subjected to a sanitary clearfelling, ASK8Jon. Also the highest values of mingling index, M_i, and domination index, U_i , were found in oak sites subjected to sanitary clearfellings (ASK8Jon and ASK10Ked) (Figure 4).

In stands disturbed by windthrows a similar process of spontaneous ecosystem regeneration was observed as in sanitary clearfellings. Usually the density of regenerating target species in cleared windthrow areas was very low, yet even in relatively similar ecosystems (windthrown spruce stands) the ratio between and abundance of regenerating target and non-target tree species were clearly different. Regeneration in the windthrow sites was also diverse (on spruce site EVK1Dub and on pine site PVK18 Dub), but birch was clearly dominating here (Figure 2). On two other windthrow sites (Figure 3) spruce was dominating on windthrown spruce site (EVK2Dub) and pine was the most abundant species on windthrown pine site (PVK14Pri) (Figure 2). Density of birch regeneration in windthrown pine sites was almost as high (PVK14Pri) or even higher (PVK18Dub) than that of pine which should be considered the main target species here. In the forest ecosystems regenerating after windthrow the lowest height of saplings was observed. Average height of seedlings on such sites did not exceed 1 m two years after the disturbance (Figure 3). The highest values of domination index U_i were found in windthrow site (EVK2Dub), while the lowest – in windthrow site (PVK18Dub) (Figure 4).

On abandoned agricultural lands the mean density of regeneration (all tree species) was not high (Figure 1). Mean density of Scots pine and silver birch differed a lot between two study sites: significantly better regeneration of the target species was observed on a more fertile site (BZU7Any) compared to a more nutrient-deficient site (BZU12Tyt). In some instances, the density of target species did not differ from that of the pioneer species in the same habitat. Silver birch and Scots pine regeneration clearly dominated on abandoned agricultural land sites; only a few seedlings of three other tree species (spruce, black alder and aspen) could be found there (Figures 2, 3). A pure birch stand has formed on a more fertile site (BZU7Any, *Oxalidosa* forest site type), where density of birch seedlings was significantly higher ($P < 0,001$) than in a mixed pine-birch stand (BZU12Tyt) (Figure 2). In developing forest ecosystems on abandoned agricultural lands birch saplings were distinguished by fast growth and average height, and on some sites, black alder saplings occured (Figure 3). Their height exceeded that of other species by nearly two times. In abandoned agricultural land the most clumped distribution ($Wi \geq 0.5$) was found on site BZU12Tyt (Figure 4).

Parameters of the equation describing *multiple dependences of abundance of regeneration* of target tree species on various ecological and biological factors are provided in Table 4. The multiple linear regression describing abundance of regeneration of Scots pine and involving eight ecological and biological factors was highly significant with quite high coefficient of determination ($P < 0.001$, $R^2 = 0.78$, Table 4). Better habitat trophotope conditions (richer soil), higher stocking level of the former stand and increased percentage of area covered by underbrush, herbs (all species) and reed-grass, and absence of vegetation cover had significant negative effects, while increased percentage of area covered by bilberry and heath had significant positive effects ($P < 0.05$) on Scots pine regeneration (Table 4).

The multiple linear regression describing regeneration of Norway spruce and involving eight ecological and biological factors was significant, however, with a moderate coefficient of determination ($P = 0.005$, $R^2 = 0.43$). Increasing stocking level of the former stand and percentage of area covered by herbs other than raspberry had significant negative effects ($P < 0.05$) on spruce regeneration; denser ground coverage by woody debris (cut branches, etc.) also had negative yet non-significant effect ($P = 0.118$) on spruce regeneration. Increased percentage of area covered by raspberry and moss had significant positive effects ($P < 0.05$; Table 4).

Regeneration of pedunculate oak, a light-demanding species preferring fertile habitats, was affected by the highest number of factors (Table 4). The multiple linear regression involved effects of eight ecological and biological factors and was highly significant with a very high coefficient of determination ($P < 0.001$, $R^2 = 0.99$). Increased values of all factors involved in the regression model, i.e., distance to a parent tree, density of coverage by tree canopies, underbrush, alder buckthorn, all species of herbs, raspberry, ferns and meadowsweet, had significant negative effects ($P < 0.001$) on oak regeneration (Table 4).

The multiple linear regression describing regeneration of common ash involved six ecological and biological factors and was highly significant with a high coefficient of determination ($P < 0.001$, $R^2 = 0.80$). Increasing percentage of area covered by common hazel, willows and alder buckthorn had significant negative effects ($P < 0.05$) on ash regeneration. Meanwhile, increasing percentage of area covered by tree canopies, wood sorrel and absence of vegetation cover had significant positive effect ($P < 0.001$; Table 4).

As the multiple linear regression shows, the integrated impact of five ecological and biological factors was highly significant in affecting regeneration of black alder (coefficient of determination $R^2 = 0.88$, $P = 0.002$). An increase of stocking level of the former stand and

Table 4. Equation parameters and estimates of multiple linear regressions describing dependencies between density of target tree species and a range of factors in regenerating/newly formed forest ecosystems (*N,* number of observations; X_i, independent variable (factor); *F,* Fisher's criterion; *P,* probability; R^2, coefficient of multiple determination; *b,* regression coefficient; *t,* Student's criterion)

Variable	*F*	*P*	R^2	*b (a)*	*t*	*P*
Scots pine (N=28)						
Free component of equation				(37882.0)	4.86	<0.001
X_1, trophotope of habitat				-2518.7	-2.85	0.010
X_2, stocking level of former stand				-19448.0	-2.59	0.018
X_5, % cover of underbrush				-199.7	-3.70	0.002
X_{10}, % cover of herbs (all species)				-98.6	-2.74	0.013
X_{11}, % cover of bilberry				81.8	2.39	0.027
X_{12}, % cover of reed-grass				-409.5	-3.97	0.001
X_{13}, % cover of heath				219.2	2.44	0.024
X_{20}, % no vegetation cover				-265.7	-3.34	0.004
Estimate of dependence	13.15	<0.001	0.78			
Norway spruce (N=28)						
Free component of equation				(36340.0)	3.37	0.003
X_2, stocking level of former stand				-47770.0	-3.59	0.002
X_3, distance to seed tree				65.0	1.85	0.079
X_{16}, % cover of raspberry				121.1	2.29	0.033
X_{18}, % cover of moss				259.4	2.71	0.013
X_{18}, % cover of other herbs				-215.1	-2.81	0.010
X_{21}, % cover of woody debris (cut branches. etc.)				-197.1	-1.63	0.118
Estimate of dependence	4.33	0.005	0.43			
Pedunculate oak (N=14)						
Free component of equation				(13519.0)	19.92	<0.001
X_3, distance to parent tree				-80.4	-26.78	<0.001
X_4, % cover of tree canopies				-190.0	-5.07	0.004
X_5, % cover of underbrush				-90.9	-14.33	<0.001
X_7, % cover of alder buckthorn				-757.3	-22.97	<0.001
X_{15}, % cover of herbs (all species)				-28.8	-4.92	0.004
X_{16}, % cover of raspberry				-531.8	-10.35	<0.001
X_{17}, % cover of ferns				-2056.1	-16.59	<0.001
X_{18}, % cover of meadowsweet				-38.1	-17.83	<0.001
Estimate of dependence	316.8	<0.001	0.99			
Common ash (N=22)						
Free component of equation				(1873.2)	4.06	0.001
X_4, % cover of tree canopies				65.0	4.34	<0.001
X_6, % cover of common hazel				-89.9	-4.00	0.001
X_8, % cover of willows				-456.8	-3.06	0.008
X_7, % cover of alder buckthorn				-599.4	-4.94	<0.001
X_{14}, % cover of wood sorrel				656.3	5.29	<0.001
X_{20}, % no vegetation cover				124.0	6.42	<0.001
Estimate of dependence	15.1	<0.001	0.80			
Black alder (N=14)						
Free component of equation				(18359.0)	3.49	0.008
X_{22}, humidity of habitat				-19684.0	-3.98	0.004
X_2, stocking level of former stand				57265	3.87	0.005
X_4, % cover of tree canopies				521.1	4.60	0.002
X_{19}, % cover of other herbs				2291.0	4.72	0.002
X_{20}, % no vegetation cover				204.0	2.41	0.043
Estimate of dependence	11.6	0.002	0.88			
Silver birch (N=13)						
Free component of equation				(7974.5)	1.17	0.281
X_{22}, humidity of habitat				16284.0	5.03	0.002
X_8, cover of willows				2869.0	5.09	0.001
X_9, % cover of herbs (all species)				-220.9	-4.26	0.004
X_{16}, % cover of raspberry				1317.2	4.79	0.002
X_{12}, % cover of reed-grass				-381.20	-3.90	0.006
Estimate of dependence	34.4	<0.001	0.96			

percentage of area covered by herbs had significant positive effects (P < 0.005) on black alder regeneration. Meanwhile, an increase in humidity of the habitat had a significant negative effect ($P < 0.005$; Table 4).

The multiple linear regression describing silver birch regeneration involved five ecological and biological factors, which integrated impact was highly significant with a high coefficient of determination ($P < 0.001$, $R^2 = 0.96$). A significant negative effect on regeneration of silver birch was observed with increasing percentage of area covered by herbs other than raspberry ($P < 0.005$). Meanwhile, an increase in humidity of habitat, as well as cover of willows contributed with a significant positive effect ($P < 0.005$; Table 4).

In general, evenness of species distribution was not high, as indicated by relatively low values of Pielou's J' and Simpson's E indices, in the investigated areas: in majority of study sites, E and J' index values did not exceed 0.5. The lowest J' index value was obtained for the abandoned agricultural land site, BZU7Any, E index value for this study site was also low, yet not the lowest among all sites (Figure 5).

A hierarchical procedure of cluster analysis revealed that regenerating ecosystems may be aggregated by their regeneration dynamics into one large group and three smaller subgroups (Figure 6). The most distant, separate small group consisted of two oak sites regenerating following sanitary clearfellings (ASK10Ked and ASK8Jon) which was mainly due to exceptionally high species diversity index values. A separate branch was represented by pure birch regeneration established on abandoned agricultural land (BZU7Any). The remaining study sites aggregated into a large cluster independently of tree species composition and type of disturbance (Figure 6).

Species diversity and evenness indices calculated for ground vegetation (herbaceous plants) in regenerating areas varied highly among sites both within and among disturbance/land-use legacy types (Figure 7). Particularly, high Shannon H' index values were obtained for ground vegetation in the ash site (USK20Kur) regenerating following sanitary clearfelling and in the black alder traditional clearcutting site (JK15Pri). In other sites, H' index did not exceed 1.4 (Figure 7). In general, on traditional clearcutting sites and on abandoned agricultural land sites Pielou's J' index values were higher compared to these calculated for sanitary clearfelling and windthrow sites. Figure 7 shows a common trend in variation of magnitude of Shannon H' and Pielou's J' indices: evenness of species representation increased with the increase in species richness. As with Shannon H' index, extremely high Simpson's D index values were obtained for the ash site (USK20Kur) and black alder site (JK15Pri), which indicates that in these sites species diversity is high and no one species is dominating. The lowest were obtained for the oak site, ASK10Ked, and the spruce site, EVK2Dub. The values of Simpson's E index corresponded well with values of Pielou's J' index (Figure 7).

Analysis of species richness of regeneration in relation to ground vegetation and shrub species (Table 5)

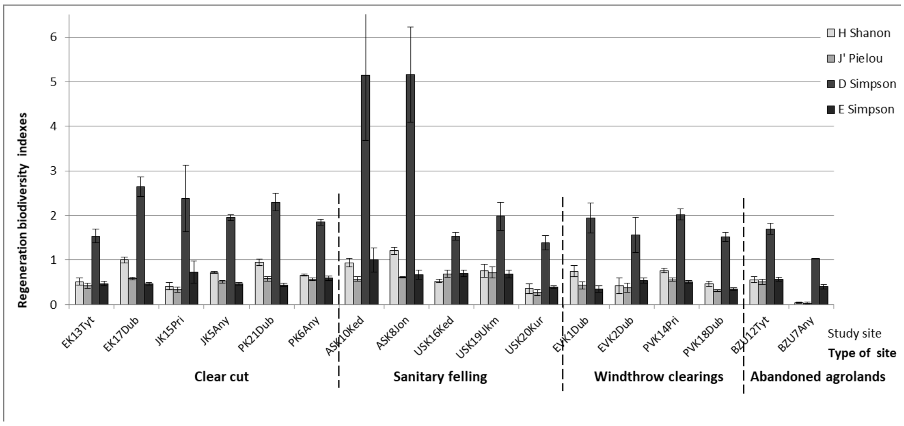

Figure 5. Species diversity and evenness indices of forest regeneration in areas affected by different types of disturbances/land-use legacies (see Table 1). Bars indicate mean values and pins indicate the standard errors

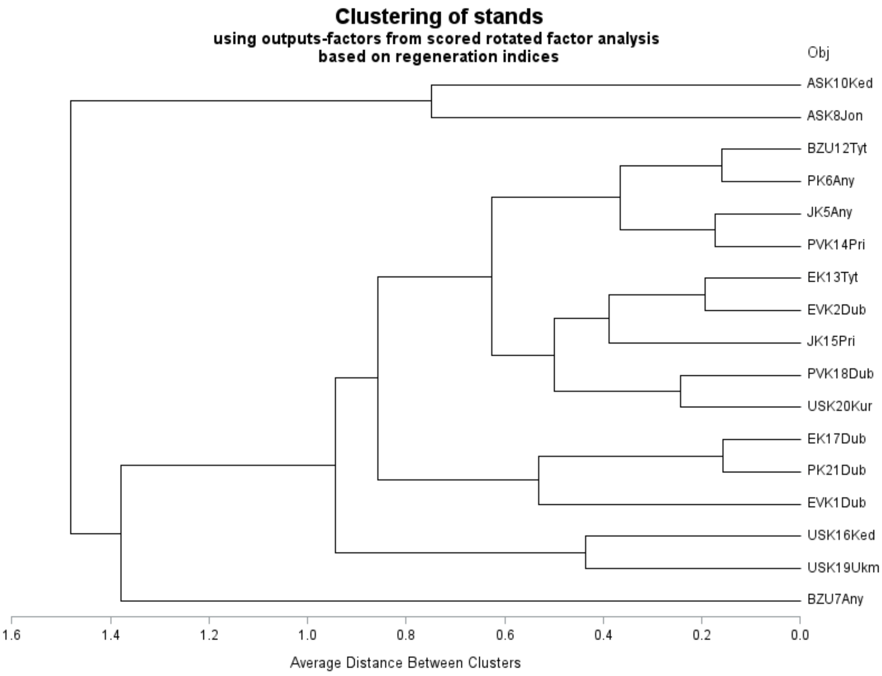

Figure 6. Aggregation of study sites (for site names see Table 1) into clusters based on factorial and cluster analysis (using FACTOR and TREE procedures) of complex of species diversity and regeneration spatial structure indices

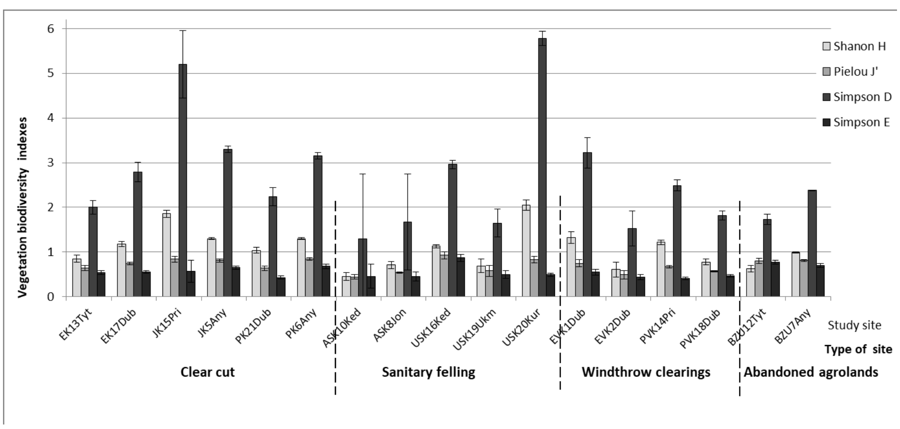

Figure 7. Species diversity and evenness indices calculated for ground vegetation (herbaceous plants) in regenerating areas affected by different types of disturbances/land-use legacies (see Table 1). Bars indicate mean values and pins indicate the standard errors

Table 5. Species richness and abundance of regeneration in relation to ground vegetation and shrub species in study sites affected by different types of disturbances/land-use legacies

Study site	Type of disturbance/ land-use legacy	Soil type	No. of tree species (TS)	No. of ground vegetation and shrub species (GVS)	Ratio GVS/TS	No. of regeneration ha^{-1} (Mean±SD)	Cover of GVS. % (Mean±SD)
EVK1Dub	Windthrow	Mesotrophic soil of normal moisture	6	26	4.3	20800±4483	94±4
EVK2Dub	Windthrow	Mesotrophic soil, temporarily overmoist	4	16	4.0	6486±1105	99±1
PVK14Pri	Windthrow	Oligotrophic soil of normal moisture	3	15	5.0	7200±1476	91±8
PVK18Dub	Windthrow	Eutrophic soil, temporarily overmoist	4	25	6.3	11429± 2727	90±10
JK5Any	Clearcutting	Oligotrophic soil, permanently overmoist	4	31	7.8	31886±4494	92±5
EK13Tyt	Clearcutting	Mesotrophic soil of normal moisture	4	20	5.0	10514±2085	94±7
PK6Any	Clearcutting	Oligotrophic soil of normal moisture	2	13	6.5	23571±2733	88±6
JK15Pri	Clearcutting	Eutrophic soil, temporarily overmoist	4	22	5.5	13543±1981	84±12
EK17Dub	Clearcutting	Mesotrophic soil, temporarily overmoist	6	21	3.5	18771±2297	92±7
PK21Dub	Clearcutting	Mesotrophic soil, temporarily overmoist	5	14	2.8	23086±5271	91±10
ASK8Jon	Sanitary felling	Eutrophic soil, temporarily overmoist	7	43	6.1	12686±1650	88±11
ASK10Ked	Sanitary felling	Eutrophic soil, temporarily overmoist	5	30	6.0	10371±1443	99±2
USK16Ked	Sanitary felling	Hypereutrophic soil, temporarily overmoist	2	26	13.0	4914±941	49±20
USK19Ukm	Sanitary felling	Hypereutrophic soil, temporarily overmoist	5	36	7.2	15775± 5129	99±1
USK20Kur	Sanitary felling	Hypereutrophic soil, temporarily overmoist	3	33	11.0	8743± 2989	94±6
BZU7Any	Abandoned agricultural land	Mesotrophic soil of normal moisture	2	30	15.0	15033±3022	99±1
BZU12Tyt	Abandoned agricultural land	Oligotrophic soil of normal moisture	2	24	12.0	7857± 1642	97±4

showed weak correlation ($r = 0.34$) between them, while the abundance of regeneration almost did not correlate with the cover of ground vegetation and shrubs ($r = 0.21$). The highest numbers of both regeneration and ground vegetation species, 7 and 43, respectively, were observed in ASK8Jon study site, a former pedunculate oak stand established on eutrophic, temporarily overmoist soil, and subjected to sanitary felling. Meanwhile, the lowest numbers of species, 2 and 13, respectively, were recorded in the site PK6Any, a clearcutting of Scots pine stand on oligotrophic soil of normal moisture.

Discussion

It is widely accepted that in the forest zone, forest ecosystems usually regenerate readily after natural disturbances (Everham, Brokaw 1996, Budzáková et al. 2013). Results of the present study also showed that forest ecosystems affected by various types of disturbances of different severity are capable to regenerate under current conditions of changing climate in the transitional zone between continental and boreal biogeographical zones although in most cases it leads to species succession. High variation in qualitative and quantitative characteristics of the regeneration has been detected among and within sites of different disturbance type. Our study shows that the number of seedlings of target tree species in a newly regenerating forest ecosystem ranged between 7–15 thous. stems per hectare which is considered sufficient for regeneration of highly productive forest ecosystems if seedling quality is good. In Lithuania, according to national legislation, area of a traditional (regular) clearcut site should not exceed 8 ha, and usually clearcut area falls within a range of 1–7 ha. Relatively small clearcut size makes preconditions for better regeneration which often benefits much from so-called edge effects, especially when the clearcutting is surrounded by mature forest stands which serve as seed sources. For example, Burton (2002) has reported highest densities of conifer seedlings in up to 70-m-wide zones stretching along north-facing forest edges.

Despite the fact that the relationship between the amount of regeneration and the distance to the nearest seed bearing individual strongly followed the negative exponential dispersal kernel that has been proposed by a number of authors (Willson 1992, Borchert et al. 2003, Greene et al. 2004), in our research, the success of the regeneration was not affected by the type of the seed source (adjacent stands, seedtree or shelterwood) and the distance to the seed source (mature seed trees). This is due to the fact that in our studies the seed source was close to the regeneration area. The exception was oak regeneration. Distance to parent tree was a highly influential factor in the regeneration of oak (t – 26.8, $P < 0.001$, Table 3). Moreover, mature stands were subjected to traditional clearcuttings, where young forest reproduction may be already present in undergrowth. This undergrowth may be used as a basis to form the future forest stand (Budzáková at al., 2013). However, we found only good quality spruce undergrowth present in clearcut areas. All other tree species were regenerated from seeds after disturbances.

Sites subjected to sanitary clearfellings may be considered as slightly less disturbed ecosystems in comparison to traditional clearfellings as some trees of other tree species and shrubs remain on site. Although if sanitary clearfelling are carried out in stands, where the disturbance agent destroys a stand before it is ready for regeneration (immature stand, no seed-bearing individuals available), or the trees have not produced seeds because of damage, the availability of local seed for regeneration may be very limited. Natural disturbances caused by biotic agents (insect pests, fungal diseases and wild game) usually affect large territories of forest stands of variable age, each of them typically specialized in certain tree species (Jõgiste et al. 2017). Regeneration of forest ecosystems heavily disturbed by biotic agents, particularly on large areas, is often problematic due to lack of desirable undergrowth and/or seed-bearing trees (Pickett et al. 1985). The results of our study showed that in sanitary clearfellings after removal of damaged trees (stands with dominating pioneer tree species) are likely to establish with only a small fraction of major/target tree species. This is due to the increased light availability which has a positive effect on the regeneration of pioneer tree species, and a large distance to the seed source of targeted tree species.

Stands disturbed by windthrows and then cleared are of similar intensity of disturbance as in sanitary clearfellings. Although amount of seed and seedling banks can be higher than it was in diseased and/or immature trees cut by sanitary fellings. Our study shows that regeneration in windthrow sites is rather substantial, which corresponds to results of astudy performed in Slovakia by Budzáková et al. (2013), which revealed that the wind-disturbed area is able to regenerate sufficiently without human intervention. In general, the density of target species in herein investigated windthrow areas was not high; nevertheless, forest ecosystem in these areas will likely regenerate quite well. The lower height of saplings in forest ecosystems regenerating after windthrows shows that regeneration proceeds slower here than on other sites. At the same time this slower process may prevent invasion of pioneer species and favour regeneration of major tree species on the disturbed sites.

Clearcuttings may be considered as severely disturbed forest ecosystems similar to ones affected by such catastrophic event as a forest fire. Because traditional clearcuttings were carried out in mature stands of high seed production, seed and seedling banks are available in place here. Our study revealed that several tree species replace the dominant tree species following clearcuttings and catastrophic natural disturbances and tend to predetermine the species composition of the future stand. The disturbed ecosystems regenerate with more than one species even on previous monoculture sites. Our findings correspond to those of other researchers (Haeussler et al. 2002), who reported that species richness in boreal forest ecosystems was 30 to 35% higher 5 to 8 years after clearcut logging than in old forest and depended on severity of silvicultural disturbances. It is widely accepted that higher species diversity predetermines higher sustainability of an ecosystem (e.g. Laliberte et al. 2010). In sites subjected to clearcutting, the amount of left dead wood, which represents a very important microhabitat for spruce regeneration (Kupferschmid and Bugmann 2005), is usually rather small. The average height of saplings two years after cutting indicates that primers of forest ecosystem have successfully established, and the risk of their destruction or deterioration is low. Saplings of such height already are in their differentiation stage (Hallikainen et al. 2007) and elements of the future stand are visible. Their natural dieback is possible due to reciprocity in case of too high stand density (Dobrowolska 2006).

Following timber removal after clearcutting or clearing of otherwise disturbed (e.g. windthrown) forest stands, light availability is improved significantly and this facilitates establishment of light-demanding species (Kobe et al. 1995, Kobe 1997, Dobrowolska 2006, Jõgiste et al. 2017). This is confirmed by our research in EVK2Dub site. After windthrow this site was not cleared, therefore, only shade tolerant Norway spruce was regenerated here. Light availability was evidently better in all our other study sites with timber extraction if compared to the condition before the disturbances.

Agricultural lands were used for agricultural production for quite a long time, e.g. several hudreds of years, and therefore can be considered as most severely disturbed ecosystems with no forest microclimate, vegetation and no forest tree seed sources available on site. Our study shows that they also can get naturally overgrown by forest if abandoned and tree seed sources are available in neigbourhood. This coresponds to findings and conclusions by previous studies (e.g. Jõgiste et al. 2017). On study sites on abandoned agricultural lands there were no seed trees therefore density of pine seedlings was relatively low but it is sufficient for the development of a new forest ecosystem. Mixed overgrowth of land with both species, birch and pine, can occur with clearly expressed groups of each species. No Norway spruce seedlings were found on abandoned agricultural lands because sites were too dry for this species and the absence of seed trees nearby.

In our study seedling heights of conifer tree species were lower than that of broadleaved species in nearly all types of regenerating forest ecosystems. We did not find clear evidence that seedlings height was influenced by the disturbance type or by competition from pioneer species. Our suggestion is that differences in heights were mostly predetermined by differences in time they appeared, i.e. their age, similar to Hallikainen et al. (2007). Several factors influence this process. One of them might be the number of seed-producing trees that survived a disturbance. However, in our study we did not find that the success of the regeneration was affected by the type of the seed source (adjacent stands, seed tree or shelterwood) and the distance to the seed source. Several ecological factors predetermine the establishment of seedlings in a regenerating ecosystem: habitat and forest type, soil conditions (Lähde 1974, Valkonen 1992, Kinnunen 1993), and development of herbaceous vegetation (Räsänen et al. 1985, Beland et al. 2000). It might be that all these factors predetermine height growth of saplings.

Evident differences in within site variation coefficients between the abundance of regeneration of target tree species and that of all tree species in a regenerating ecosystem may show a trend that forest structurization and species diversity increase in the consequense of natural disturbances as regeneration involves admixtures of other tree species conditioning high probability of species succession. Our study has revealed that in spruce clearcutting sites the number of seedlings of non-target species reaches 3–8 thous. stems per hectare. This amount can compete with spruce. There is a high probability that two-layer stands will establish on spruce cutting sites with birch occurring in the first layer and spruce, as a slower growing and shade-tolerant species, remaining under it. Admixture of other tree species on spruce cutting sites is not essential. Thus, regeneration of spruce stands after clearcuttings will most often involve other tree species with silver birch prevailing among them. This is often the case in the sub-boreal spruce zone (Burton 2002, Jonášová et al. 2007).

According to Kinnunen (1993), and Hallikainen et al. (2007), because of faster growth rate at an early age, birch will occur in the upper layer and will shade also pine seedlings. Therefore, regeneration of pine stands on their clearcutting sites gets problematic if no species composition control measures are applied. There is the highest probability of species succession during regeneration of these ecosystems and it is likely that future stands will be composed of more than three tree species. On some sites, pure pine stands can establish if adequate seed sources exist nearby (Kinnunen 1993).

In general, in our experience, the diversity of sapling heights in ecosystems regenerating after natural disturbances usually is moderate or, in separate cases, low. In the early stage of ecosystem regeneration, the interaction between saplings does not occur or, at least, is not evident, as ecosystem still has not passed from the individual development of trees to the development in a community (Hallikainen et al. 2007). Therefore, height differentiation of saplings is more often predefined by species diversity, differences in seeding time, species-specific growth rates but not infraspecific or interspecific competition.

Research carried out in northeastern Poland found that forest regeneration pattern depended on stand disturbance degree – the overall structural diversity index – showed that stand regeneration in the slightly or moderately disturbed stands was more differentiated than the young growth in the severely disturbed stands (Szmyt and Dobrowolska 2016). Szmyt and Dobrowolska (2016) found that only pine saplings were nearly pure or shape pure tree groups in ecosystems regenerating after catastrophic natural disturbances. Meanwhile, the most random distribution in our study is observed in oak saplings. This could be predefined by the specific distribution pattern of oak as acorns are usually dispersed by small rodents and birds (Jones 1959, Ducousso and Bordacs 2004). It is considered that U_i d” 0.40 indicates low, 0.40 < U_i d”0.60 indicates moderate, and U_i > 0.60 high differentiation of heights (Vorčak et al, 2006). Thus, height differentiation of oak saplings should be considered as very high.

In most plots Simpson's D index was low, showing that single or two species are dominating and will form the basis for future stand. Their aggregation into clusters could be due to low regenerating species diversity, related to the type of habitat, species composition of the original stand, and, at a lesser extent, to the type of disturbance suffered.

Evenness of distribution of saplings of some tree species is related with the intensity of disturbance. Our study revealed that the heterogeneity of a new forest ecosystem is at least partly conditioned by the type of disturbance. Segregation of oak stands into a separate group could be predetermined by specific environmental conditions typical for mixed oak stands for natural species-rich regrowth to proceed after the disturbance. Kuuluvainen and Juntunen (1998) have found that birch regenerates unevenly in severely windthrown ecosystems independent of whether the area cleaned of windthrows or not. Meanwhile, in case of moderate disturbances, regeneration of birch occurs more evenly. This is explained by the fact that in moderately disturbed ecosystems birch is not uprooted but usually only windbroken or windsnapped, and still can produce seeds for some time. Although it is evident that natural disturbances have some influence on structure of saplings, however, literature sources almost do not provide data on how natural disturbances influence height of regenerating saplings. According to Szmyt and Dobrowolska (2016), more even saplings regarding their height establish after severe natural disturbances, and less even in less affected ecosystems. In general, saplings shape groups by height with prevailing broadleaved species, seeds of which distribute readily within the area of a regenerating ecosystem (Dobrowolska 2015).

Ground vegetation is often treated as an obstacle to natural forest regeneration. However, in our study we detected a very weak positive correlation (r = 0.21) between ground vegetation cover and abundance of regeneration. The study demonstrated that species composition of ground cover depends not only on climatic and soil conditions but also on peculiarities of forest stand, type of disturbance and preceding human activity. In our study, the number of ground vegetation species varied within a range from 13 to 43 and was weakly correlated with the number of regeneration species (r = 0.34). As a rule, higher abundance of species was observed on sanitary felling sites which were distinguished by fertile soils (eutrophic and hypereutrophic types). A very similar pattern could be observed with the cover percentage, unless any significant amounts of deadwood or woody debris was left in a site.

The value of Shannon's E index and assessment of plant cover indicates that ground vegetation occupies whole sites relatively evenly, and a continuous cover of herbs, mosses and shrubs establish in most of the study sites. The intensity and pattern of the overgrowth is much related to the type of habitat, as mentioned above. This kind of relationship was also reported by Roberts and Gilliam (2014), who found that the patterns of diversity indices depended on site type, with no difference on dry-mesic sites and greater S and H' in clearcuttings compared to controls on mesic sites in northern lower Michigan.

A report from eastern Poland (Kuijper et al. 2010) showed that herbaceous vegetation cover was the main factor determining the number of seedlings with an optimum at 38% of cover in the Białowieza Primeval Forest. In our study the highest numbers of regeneration were observed in the sites, where ground vegetation cover amounted to about 90%. This discrepancy is likely to be explained by different measurement techniques applied or species range included in the two studies. Our results are not fully in favour with those of Budzáková et al. (2013), higher diversity of herbaceous vegetation was found in areas disturbed by heavy windthrows but not cleared from deadwood. For instance, the EVK2Dub, a windthrow site with deadwood left on the ground, contained only 16 ground vegetation species with *Rubus idaeus* alone covering 85% of the site. In highly disturbed forest ecosystems, effective population size decreases and therefore the genetic diversity of stand-forming tree species may decrease, and this may result in poor physiological and genetic adaptation as well as reduced sustainability of the respective populations (Lande and Rarrowclough 1996).

Conclusions

Results of the present study showed that forest readily regenerated in all investigated study sites irrespective of disturbance/change of land-use legacy. However, high variation in qualitative and quantitative characteristics of the regeneration was detected among sites leading to a wide spectrum of newly forming forest communities that in most cases were largely different from the previous (undisturbed) communities. A clear trend of species succession is easily observable already at the early stage of community development. Species composition of the regenerating forest ecosystems depends on those prevailed before disturbance, however, the pioneer species – silver birch, Scots pine, black alder, etc. – typical for the disturbed ecosystems out-compete the others.

The most intensive forest regeneration takes place in those forest ecosystems which were subjected to direct human impact, i.e. clearcuttings, and less intensive regeneration, particularly, that with target species – on sites cleared of windthrows and where sanitary fellings were applied. Although non-target species regarding habitat type usually prevailed on cutting sites, however, numbers of saplings of target species were sufficient for the regeneration of high productivity forest ecosystems and development of the new ones. Abundance of regenerating target species in most of the studied ecosystems was in favour with biological diversity and species survival, although, formation of high productivity stands requires intervention with silvicultural measures to control the abundance of competing pioneer tree and herbaceous species.

Multivariate regression analysis revealed that regeneration of different tree species is influenced by different sets of local biotic and abiotic conditions. Out of the studied scores of factors, the abundance of regeneration was reliably described by an integrated impact of 5 to 8 factors, which usually had negative effects on regeneration: distance to parent tree, higher stocking level of the original stand, large amounts of deadwood remained, cover of canopy, underbrush and herbaceous species, etc.

Variation in abundance of regeneration, its spatial evenness, growth differentiation and tree species mingling, were related to high variation of growth microconditions due to patchy structure and occurrence of herbaceous vegetation which might be promoted by temperature and humidity extremes occurring in large opennings in disturbed forest ecosystems as the consequence of climate change. Analysis of biodiversity indices revealed that in most studied disturbed or demolished forest ecosystems only a single or two tree species dominated and will form the basis for the future stand, meanwhile broadleaved tree stands on the sites subjected to sanitary fellings have high species diversity and no dominance by single species was present. Although the pioneer herbaceous species establish on areas affected by natural disturbances, they do not fully prevent the regeneration process, instead they influence its progress, evenness and species composition of the future forest communities.

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