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ORIGINAL PAPER

Succession of ground beetle (Coleoptera: Carabidae) communities after windthrow disturbance in a montane Norway spruce forest in the Hrubý Jeseník Mts. (Czech Republic)

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Abstract
Wind disturbances are a key factor that is significantly involved in the life cycle of natural boreomontane coniferous forests. As most of these forests are currently intensively managed, we have limited knowledge on succession following natural disturbance. Succession in a Norway spruce stand after a windthrow event was studied using ground beetles as model bioindication taxa in the Hrubý Jeseník Mts. (Czech Republic). The study documented that the composition of ground beetle communities was significantly associated with stand age and its microclimatic parameters (particularly the minimal temperature and average and minimal humidity). Forest species including prey specialists, hygrophilous species, as well as habitat generalists were the most abundant in the mature stand, where the forest had the highest humidity and the least profound minimal temperatures. In contrast, open-habitat species, including euryoecious species and relict species of higher elevations, reached their highest abundances in clearing shortly after the windthrow. In clearing the humidity was lower and the temperature fluctuated significantly (the lowest minimal temperatures). Ground beetles, including forest species, were the least abundant in young stands (10 and 20 years after windthrow). We conclude that old stands are of particular importance because they harbour the highest abundance and diversity of ground beetles with various ecological requirements. Natural wind disturbances are important as well since they increase diversity by enabling the occurrence of many non-forest species. Hence, a mosaic of stands of different ages with a sufficient proportion of old stands should be maintained when managing montane coniferous forests.

Key words: forest stand development; microclimate; multivariate analysis, windstorm

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1. Introduction

Natural disturbances, such as windthrows, are key factors in the process of regeneration in continuity of coniferous temperate and boreal forests (Peterken 1996). As trees are broken or uprooted and open tree-fall gaps arise, the stable conditions of shady forest ecosystems are disrupted. Tree-fall gaps are characterised by bare patches of mineral soil, high amounts of dead wood, and increased sunlight reaching the forest floor. Thus, windthrows are followed by important changes in microclimate, ground structural heterogeneity and vegetation. These changes significantly affect the invertebrate fauna (Bouget & Duelli 2004).

Ground beetles (Carabidae) as a model bioindication group (Rainio & Nimelä 2003) are among the most studied invertebrates, and thus the succession of their communities within the traditional forest management cycle from clear-cutting (i.e., artificial disturbance) to mature stands is also well studied (e.g., Butterfield 1997; Koivula et al. 2002; Magura et al. 2003; Purchart et al. 2013). In general, changes in ground beetle communities after natural disturbances (e.g., windthrows) are insufficiently studied (Sklodowski & Garbalińska 2007). However, some studies dealing with this topic have been conducted in the Alps (Duelli et al. 2002; Winter et al. 2015), northern Poland (Sklodowski & Garbalińska 2007), the Tatra Mountains (Urbanovičová et al. 2010; Šustek & Vido 2013) and North America (Gandhi et al. 2008). The results of these studies can be summarised into three main outcomes: i) windthrows are followed by decreased abundances of forest species, ii) tree-fall gaps are characterised by the occurrence of species specific to open habitats, and iii) changes in temperature

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and humidity are considered to be the most significant factors driving ground beetle community succession in these studies.

Although climatic factors (above all, temperature and humidity) are considered to substantially affect the succession of ground beetle communities after windthrows (see above), the exact relationships between changes in climatic factors and beetle succession were not addressed in the aforementioned studies. In addition, a majority of these studies were carried out in mountains, where climatic factors largely limit insect survival (Mani 1968). Therefore, the present study investigates the effects of selected forest stand characteristics and climatic factors on communities of ground beetles in a montane coniferous forest after windthrow. The following hypotheses were tested: i) ground beetle species composition and abundace are affected by forest disturbance by windthrow and its following regeneration and ii) ground beetle species composition and abundace are affected by habitat temperature and humidity. Both hypotheses were tested at the community, ecological guild and species levels. Based on our obtained results, we suggest implications for forestry management.

2. Methods

2.1. Study site

The study area is located in northern Moravia (the Czech Republic) in the Jeseníky Protected Landscape Area, and is 2 km east of Praděd Mt. (1492 m a. s. l), near the Kamzičí chata cottage, at an elevation of 1200 – 1220 m a. s. l. (50.0820747N, 17.2619078E). The locality is situated in a seminatural montane spruce forest. The climate is cold, with a mean temperature of 1.9 °C, the long-term annual average rainfall is 1100 – 1200 mm, and snow cover lasts approximately 180 days, typically from November to early May (Quitt 1971).

We sampled four stands of different ages with areas ranging 2 – 5 ha, each stand representing a different stage of succession of spruce forest after windthrow of a mature stand: i) clearing 3 years after the event (hereafter "3"), ii) stand approximately 10 years after the event, young growth ("10"), iii) stand approximately 20 years after the event, young stand ("20"), iv) stand approximately 90 years old, mature stand ("90"). Following windthrow, the surviving trees (a few trees per ha) were kept in situ, but a majority of the dead wood caused by the windthrows or bark beetles was removed from the stands. As a result, a low amount of coarse dead wood was present in the studied stands. The studied stands were established by natural regeneration following the windstorm events, which was supported by artificial regeneration. The study stands were dominated by Norway spruce (*Picea abies* [L.] H. Karst.) (90%) with dispersed individuals of rowan (*Sorbus* sp.), European beech (*Fagus sylvatica* L.) and birch (*Betula pendula* Roth.).

2.2. Field sampling and variable measurement

Ground beetles were sampled using pitfall traps (8 cm in diameter, 15 cm deep, one-third filled with a 4% formaldehyde solution), a standard method used to sample epigeic invertebrates (Spence & Niemelä 1994). In each study stand, 8 traps were installed in a line at a spacing of 10 m. The trap lines were located in the centres of the study stands, and no trap was closer than 10 m from the stand edge. In total, 32 traps were used. The pitfall traps were exposed from 30. 5. to 16. 10. 2011 and were emptied at approximately three-week interval (21. 6., 9. 7., 27. 7., 14. 8., 1. 9., 19. 9. and 16. 10. 2011). Each sample was preserved in 95% ethanol. All ground beetles were identified to the species level using keys (Hůrka 1996). The used nomenclature follows de Jong (2012).

Additionally, one datalogger (Voltcraft DL-120TH) was installed in the middle of each study stand and was active during the whole period of beetle trapping. Dataloggers were mounted 10 cm above the ground in a shaded location. The dataloggers recorded the following climatic characteristics: minimal daily temperature (hereafter "Tmin"), average daily temperature ("Tave"), maximal daily temperature ("Tmax"), minimal daily humidity ("Hmin") and average daily humidity ("Have").

2.3. Data analysis

Prior to data analysis, the number of individuals of each species per sample was converted to the number of individuals per sampling day (relative abundance) to remove possible bias caused by the slightly uneven lengths of the trap exposure intervals. For each interval of trap exposure, the mean values of the explanatory climatic variables (Tmin, Tave, Tmax, Hmin, Have) were calculated and coded as continuous variables.

To relate gradients in species composition and abundance to the studied predictors and to test the importance of these predictors, a canonical correspondence analysis (CCA) was used (ter Braak & Šmilauer 2002), which is appropriate for data with a larger gradient length (the gradient length was previously examined by detrended correspondence analysis (DCA)). The data were standardised and centred by sample, and a Monte Carlo permutation test was used (2000 permutations). All the explanatory variables (i.e., climatic variables and stand age) were treated as continuous variables. The four sampled stands (i.e., 3, 10, 20, 90) were treated as supplementary variables in the analysis. A forward selection procedure was used to the test environmental variables. Since ground beetle communities are strongly affected by phenology (Rainio & Niemelä 2003), we treated the date of sample collection (coded as an ordinal week of the year) as a covariate.

Subsequently, we used generalised linear models (GLMs) with a Poisson distribution and log link function to separately assess the impact of selected single factors on particular species. The most significant factors according to the results of CCA were selected, which were stand age, Tmin and Have. Only species with at least 5 specimens recorded were tested by GLM. All these analyses were conducted using CANOCO, v. 4.5. (ter Braak & Šmilauer 2002).

Furthermore, we also studied differences in the abundance of particular ecological guilds of ground beetles among the various stages of forest succession. All species were divided into three guilds according to their habitat association: forest specialist, open-habitat specialist or habitat generalist (Hůrka 1996; Kašák et al. 2015). Since the resulting data on guild abundances did not exhibit a normal distribution (Shapiro-Wilk test), non-parametric Kruskal-Wallis (K–W) tests supplemented with box and whisker plots were used (Hollander & Wolfe 1999). These tests were performed in Statistica 10.0 (StatSoft 2013).

3. Results

In total, 2703 individuals of ground beetles belonging to 31 species were recorded. The most abundant species were *Carabus linnaei*, with 792 individuals, followed by *Carabus auronitens*, *C. sylvestris*, *C. violaceus*, *Pterostichus unctulatus* and *Trechus striatulus*, all with more than 100 specimens sampled. Among the others, several relict species, indicating naturally rich sites, were recorded: *Amara erratica*, *Cychrus attenuatus* and *Pterostichus rufitarsis cordatus*. The sampled ground beetle communities consisted of three different beetle guilds: a) forest species that predominated in the community (18 species represented by 1925 individuals), b) generalists (7 species represented by 455 individuals) and c) open-habitat species (6 species represented by 323 individuals). The numbers of species recorded in the different studied stands were similar, but the abundances of individuals differed remarkably: stand 90 – 1717 individuals/20 species; stand 20 – 228/19; stand 10 – 261/20; stand 3 – 497/23.

3.1 Community pattern of ground beetles

The CCA model revealed that the composition of ground beetle communities was significantly associated with stand age and climatic factors (Table 1, Fig. 1,). Among the tested factors, stand age exhibited the highest explanatory power (Table 1). The most important climatic factors were minimal temperature and average and minimal humidity (Tmin, Have and Hmin).

The longest gradient of species data in the CCA plot (Fig. 1) can be seen along the horizontal canonical axis and corresponds to the environmental changes from young stands to mature stands with a more stable microclimatic environment and higher minimal temperature and humidity. The forest species typical of mature stands (*Calathus micropterus*, *Carabus auronitens*, *C. glabratus* and *C. linnaei*) predominated on the left side of the plot, whereas habitat generalists and open-habitat species (*Amara lunicollis*, *Carabus violaceus*, *Leistus ferrugineus*, *Notiophilus palustris*, etc.) were bound to the right side of the plot. Simultaneously, hygrophilous species (*Patrobus atrorufus*, *Trechus striatulus* and *T. splendens*) were associated with the left side of the plot, whereas euryoecious species tolerant of dry conditions (*Bembidion lampros*, *B. quadrimaculatum* and *Leistus ferrugineus*) were shown on the right side of the plot. Further, relict species from higher altitudes (*Amara erratica* and *Carabus sylvestris*) that are usually bound to nearby alpine habitats were also positioned on the right side of the plot.

Table 1 Results of canonical correspondence analysis. Effect of age of spruce stands and abiotic variables on communities of ground beetles.

Variable	F	Explained variability [%]
Age	11.21***	6.15
Tmin	2.06**	5.46
Have	2.25**	5.12
Hmin	2.98***	4.12
Tave	1.12ns	4.09
Tmax	0.91ns	2.56

ns not significant; *** p < 0.001; ** p < 0.01; * p < 0.05

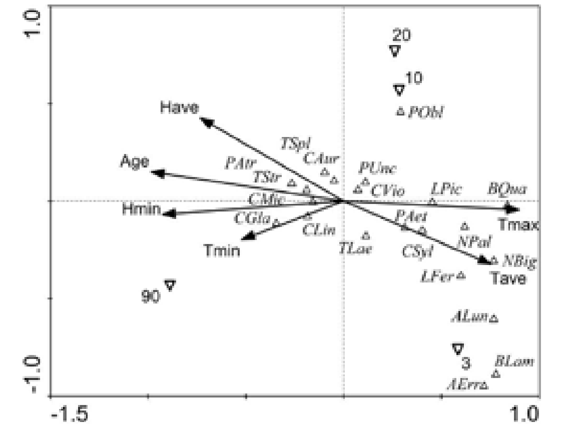

Fig. 1. Canonical correspondence analysis – triplot of associations between ground beetle occurrence in montane Norway spruce forest of Hrubý Jeseník Mts. and environmental variables (stand age and climatic variables), with supplementary environmental variables (the sampled 3-, 10-, 20- and 90-year-old stands) shown. Environmental variables are denoted as filled black arrows, supplementary (passive) variables are denoted as open downward pointing triangles. Only species with fit range > 2% are depicted in the ordination plot. The beetle species are denoted by open upward pointing triangles with corresponding abbreviations: *Amara erratica* (AErr), *Amara lunicollis* (ALun), *Bembidion lampros* (BLam), *Bembidion quadrimaculatum* (BQua), *Calathus micropterus* (CMic), *Carabus auronitens* (CAur), *Carabus glabratus* (CGla), *Carabus linnaei* (CLin), *Carabus sylvestris* (CSyl), *Carabus violaceus* (CVio), *Leistus ferrugineus* (LFer), *Leistus piceus* (LPic), *Notiophilus biguttatus* (NBig), *Notiophilus palustris* (NPal), *Patrobus atrorufus* (PAtr), *Pterostichus aethiops* (PAet), *Pterostichus oblongopunctatus* (PObl), *Trechus splendens* (TSpl), *Trechus striatulus* (TStr), *Trichotichnus laevicollis* (TLae).

3.2. Responses of specific groups of ground beetles to stand age

The results of the K–W tests revealed that the abundance of ground beetle guilds differed significantly among stands of different ages (Fig. 2). The biggest differences were found in the occurrence of the guild of forest species, which reached its highest abundance by far in the mature 90-year-old stand. Open-habitat ground beetles were the most abundant in the youngest 3-year-old stand, less abundant in the mature 90-year-old stand and almost absent in the 10- and 20-year-old stands. Habitat generalists were the most abundant in the 90-year-old stand.

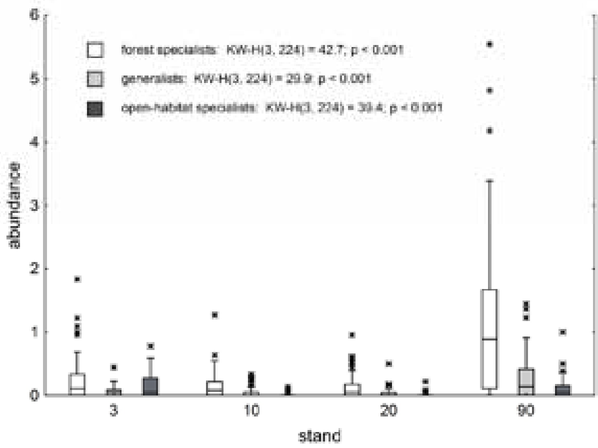

Fig. 2. Differences in abundance of three ecological guilds of ground beetles among stands in different stages of forest succession following windthrow in montane Norway spruce stand of Hrubý Jeseník Mts. On the x axis is age of stand in years. The box and whisker plots are composed of outliers (asterisks), non-outlier ranges (whiskers), lower and upper quartiles (boxes) and medians (middle lines). Results of Kruskal-Wallis tests are shown as well.

3.3. Responses of ground beetle species to stand characteristics

Using GLM analyses, the occurrences of 19 species of ground beetles were found to be significantly affected by at least one of the tested habitat factors (Table 2). Specifically, 18 species responded significantly to stand age (12 increased in abundance, 6 decreased), 12 were affected by the minimal temperature (all increased), and 12 varied in abundance according to the average humidity (9 increased, 3 decreased).

Thus, typical forest ground beetles increased in abundance in stands of higher age, which was particularly remarkable in the case of species of the genus *Carabus* and food specialists that prey on molluscs, such as *Cychrus caraboides* and *C. attenuates* (Table 2). In contrast, the abundance of open-habitat species (*Amara* spp. and *Carabus sylvestris*) and some euryoecious species (e.g., *Leistus ferrugineus* and *Notiophilus palustris*) that are associated with disturbed open habitats, such

Table 2. Results of generalised linear model analyses for beetles and their responses to different features of spruce stands.

Species	N	Age				Tmin				Have			
		F^a	Intercept	Slope	AIC	F^a	Intercept	Slope	AIC	F^a	Intercept	Slope	AIC
Amara lunicollis	6	**48,47*****	−14	−0,06	1,45	0,42^{ns}	1,12	0,14	2,43	7,22***	−13,29	0,61	2,05
Calathus micropterus	90	**28,96*****	1,8	1,05	11,55	**11,71*****	2,96	0,86	13,96	**7,37****	9,96	0,82	14,51
Carabus auronitens	123	**30,64*****	1,3	1,69	15,91	**19,47*****	4,09	1,01	16,87	**9,27****	10,72	1	18,16
Carabus glabratus	6	**38,53*****	12,44	0,09	1,63	1,35^{ns}	2,59	0,22	2,51	**3,51***	22,94	0,34	2,36
Carabus linnaei	792	**43,57*****	1,94	5,18	76,12	**25,45*****	5,17	2,74	96,42	**8,72****	10,02	2,45	109,24
Carabus sylvestris	312	**2,83***	−0,34	−0,87	35,46	**8,63*****	1,46	1,26	33,98	3,01^{ns}	−3,43	−0,94	35,41
Carabus violaceus	164	**6,66***	0,52	0,95	18,62	**18,99*****	2,67	1,11	17,11	0,96^{ns}	2,43	0,38	19,47
Cychrus attenuatus	7	**47,77*****	12,66	0,09	1,75	**13,06*****	19,77	0,44	2,26	0,71^{ns}	7,44	0,19	2,81
Cychrus caraboides	15	**9,29****	1,41	0,63	3,78	**10,32*****	5,96	0,39	3,8	**6,29***	15,63	0,43	3,96
Leistus ferrugineus	13	**8,63*****	−2,17	−0,74	3,71	1,16^{ns}	−0,91	−0,35	4,43	12,77***	−14,3	−1	3,55
Leistus piceus	31	**6,25****	−0,98	−0,74	7,41	0,03^{ns}	0,14	0,06	8,05	2,45^{ns}	−5,65	−0,54	7,79
Notiophilus biguttatus	10	**131,97*****	−13,48	−0,1	1,66	0,04^{ns}	−0,17	−0,05	3,27	14,76***	−12,68	−0,77	2,67
Notiophilus palustris	10	**7,58*****	−1,68	−0,57	2,96	0,06^{ns}	0,27	0,06	3,44	3,03^{ns}	−8,72	−0,5	3,24
Patrobus atrorufus	17	**24,04*****	3,52	0,75	3,07	**6,89*****	6,57	0,41	4,84	**3,90***	16,87	0,49	5,07
Pterostichus aethiops	5	1,59^{ns}	−0,48	−0,15	1,77	0,51^{ns}	1,16	0,13	1,77	0,94^{ns}	−6,12	−0,22	1,75
Pterostichus diligens	13	**0,00***	0,04	0,02	4,68	0,40^{ns}	1,14	0,21	4,56	0,43^{ns}	6,8	0,23	4,59
Pterostichus oblongopunctatus	80	0,18^{ns}	0,12	0,15	13,57	1,12^{ns}	0,64	1,81	13,43	2,23^{ns}	5,27	0,49	13,29
Pterostichus rufitarsis	17	0,03^{ns}	0,08	0,05	4,72	0,08^{ns}	0,26	0,07	4,71	0,09^{ns}	−4,19	−0,27	4,64
Pterostichus unctulatus	615	**12,86*****	0,73	2,39	60,34	**14,70*****	2,29	2,04	59,41	**3,51***	4,97	1,28	64,86
Trechus splendens	91	**23,27*****	1,53	1,58	15,11	**6,97*****	2,79	0,85	17,28	7,61***	14,6	1,02	17,13
Trechus striatulus	236	**59,48*****	2,23	2,89	28,32	**7,73*****	2,64	1,34	40,04	**15,12*****	18,06	1,84	37,77
Trichotichnus laevicollis	37	0,83^{ns}	0,35	0,3	8,38	**4,67****	2,29	0,52	7,95	4,62^{ns}	−2,77	−0,26	8,35

^{ns} not significant; *** p < 0.001; ** p < 0.01; * p < 0.05; p-values in bold are significant at $\alpha = \leq 0.05$; positive responses of species to the tested environmental variables are highlighted by a grey background.

as windthrow gaps, decreased in stands of higher age. Increasing humidity was associated with higher abundances of hygrophilous species of the genus *Trechus* and some forest species of the genus *Carabus*.

4. Discussion

Our results confirm that windstorm events in Norway spruce mountain forest and subsequent forest regeneration and succession are associated with dramatic changes in ground beetle communities. Among the tested factors, stand age (i.e., time elapsed after windthrow event), minimal temperature and average humidity affected ground beetles the most significantly (Table 1). In general, the abundance of forest species increased with an increase in the age of the stand. However, this increase is likely not linear but instead commences later in succession because the abundances of forest species were even slightly lower in 10- and 20-year-old stands (Fig. 2). Thus, forest ground beetles, as well as ground beetles in total, reached maximal abundances in the mature 90-year-old stand, which was characterised by the highest values of minimal temperature and average humidity. In contrast, open-habitat species and euryoecious species occurred most numerously in the clearing 3 years after windthrow. These results are in accordance with previous studies on carabid succession after wind disturbances (Šustek & Vido 2013; Winter et al. 2015) or during the standard forestry cycle (Magura et al. 2003).

A decrease in the abundance of forest ground beetles following windthrow or felling is explained mainly by dramatic changes in abiotic conditions (Koivula et al. 2002; Sklodowski & Garbalinska 2007). It is believed that forest ground beetles require a relatively stable microclimate (Thiele 1977). Such conditions are better maintained in mature (or undisturbed) forest stands, which protect the ground against direct sun and wind exposure due the higher canopy closure (Sklodowski 2017). In contrast, the temperature fluctuates strongly in windthrow gaps or clear-cut areas (Chen et al. 1999), where high temperatures might be reached during a sunny day but temperatures decrease substantially at night or during a windy and cloudy day (Warren & Key 1991). In accordance, the highest minimal temperatures, reflecting the most stable microclimate, were maintained in the mature stands in the present study, where the highest abundance of forest ground beetles was also found (Fig. 1 and 2). Furthermore, our study documented the minimal temperature to be a more important climatic factor than average temperature (Table 1). Correspondingly, the survival and reproduction of animals are mostly affected by extreme values of habitat characteristics rather than by average values (Begon et al. 2006).

The aforementioned increased sun and wind exposure of the ground after windthrow or felling lead to lowered humidity (regardless of a higher total amount of rainfall) (Ishizuka et al. 2002). Subsequently, as the canopy densifies during succession in a new forest stand, the humidity rises again, as was documented in the present study (Fig. 1), leading to increased abundances of hygrophilous forest ground beetles, such as *Trechus* spp., which were more numerous in the older stands (90 years old) in the present study (Fig. 1, Table 2). Similarly, in the present study, species of the genus *Cychrus* that feed upon molluscs (Hůrka 1996) also experienced an increase in abundance in older stands. The molluscs were previously reported to diminish after windthrow events due to lower humidity (Duelli et al. 2002). In the present study, the mature forest stand (90 years old), with the most stable climatic conditions (including a smaller range of extreme values), hosted the highest numbers of forest ground beetles as well as all ground beetles in total. Ground beetles may also prefer old stands because woody debris and litter provide shelter and preserve microhabitat conditions (Sklodowski 2016). Similar results were reported by Urbanovičová et al. (2010) in the Tatra Mts., showing the highest abundance of ground beetles in undisturbed forest stands.

Despite the substantial decrease in the abundance of forest ground beetles after windthrow, the abundance of forest ground beetles remained higher in the windthrow clearing (3 years after the event) than in slightly older (10- and 20-year-old) forest stands. This phenomenon has also been documented in other similar studies (Magura et al. 2003; Purchart et al. 2013; Sklodowski 2017), and it can be explained by the following: a) some ground beetle species (members of the genus *Carabus*) can survive several years in suboptimal habitats (Koivula et al. 2002) because their development takes several years (Hůrka 1996), and adults can live for a few years as well; b) a windthrow area might temporarily offer high numbers of prey because an open habitat with a substantial amount of freshly dead wood and an array of herbs is characterised by a high abundance of saproxylic and herbivorous invertebrates (Winter et al. 2015; Sklodowski 2017) c) temporarily increased amount of dead wood provides shelter for carabids (Sklodowski 2016; Sklodowski 2017).

Overall, the lowest abundances of forest ground beetles were recorded in 10- and 20-year-old stands in the present study (Fig. 2). Similarly, a decrease in abundance of forest ground beetles during the first half of the forest life cycle has been observed in several studies (Butterfield 1997; Magura et al. 2003; Purchart et al. 2013). This might be attributed to the fact that forest stands in this stage are usually very shady with a negligible amount of dead wood and a poorly developed herbaceous understorey (Purchart et al. 2013), so the supply of prey and shelters in such habitats is strongly limited (Taboada et al. 2008).

As expected, open-habitat ground beetle species reached their highest abundance in the clearing 3 years after windthrow, which corresponds to the results of other studies (Sklodowski & Garbalińska 2007; Gandhi et al. 2008; Šustek &Vido 2013; Sklodowski 2017). The second highest abundance of open-habitat species was surprisingly found in the mature 90-year-old stand. This corresponds to the fact that mature montane spruce forests usually exhibit a partly open structure because their canopies are already disturbed by dieback or falling/felling of individual trees (Winter et al. 2015).

The clearing (3 years after windthrow) hosted the highest abundance of open-habitat species (*Amara* spp. and *Harpalus* spp.) and euryoecious ground beetles typical of disturbed habitats (*Bembidion lampros*, *B. quadrimaculatum, Leistus ferrugineus* and *Notiophilus palustris*). Several important bioindicator species, such as the boreomontane species *Amara erratica* and *Carabus sylvestris*, which are typically distributed in alpine meadows (Stanovský & Pulpán 2006), occurred in the clearing as well. Clearings after windthrows represent temporarily open habitats that can enable the reproduction of these species. Additionally, these species could easily colonise the clearing at our study site because of its proximity to alpine meadows in the Hrubý Jeseník Mts., where they are quite numerous (cf. Kašák et al. 2015).

5. Conclusion

Based on the results of the present, , as well as several other studies (Magura et al. 2003; Niemelä et al. 2007), we can assume that the presence of old forest stands at a particular location is a fundamental prerequisite for the long-term survival of populations of specialised forest ground beetles. At the same time, newly regenerated forest stands after a windthrow event or felling do not become optimal for forest ground beetles until they are 60 – 90 years old. Therefore, montane forests should be managed to ensure that a sufficient area of mature forest stands is maintained near any clearing until the clearing becomes a middle-age-class stand. On the other hand, disturbed areas, such as windthrow clearings, support the occurrence of many non-forest species (e.g., open-habitat, euryoecious species) and thereby increase the overall diversity of ground beetles in these ecosystems. Hence, a fine mosaic of forest stands of various ages can enable the contemporary survival of many different ground beetle ecological groups and species.

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Appendix 1. Abundances of the ground beetles sampled in the Hrubý Jeseník Mts. and their ecological characteristics.

Species	H[a]	R[b]	Age of stand				Total
			3	10	20	90	
Amara erratica (Duftschmid, 1812)	O	R	2	0	0	0	2
Amara lunicollis Schiödte, 1837	O	A	6	0	0	0	6
Bembidion lampros (Herbst, 1784)	O	E	1	0	0	0	1
Bembidion quadrimaculatum (Linnaeus, 1761)	O	E	1	0	0	0	1
Calathus micropterus (Duftschmid, 1812)	F	A	10	4	1	75	90
Carabus arvensis (Herbst, 1784)	G	A	2	0	0	1	3
Carabus auronitens Fabricius, 1792	F	A	10	14	20	79	123
Carabus glabratus Paykull, 1790	F	A	0	0	0	6	6
Carabus intricatus Linnaeus, 1761	F	A	1	0	0	0	1
Carabus linnaei Panzer, 1810	F	A	89	5	17	681	792
Carabus sylvestris Panzer, 1793	O	A	157	16	19	120	312
Carabus violaceus Linnaeus, 1758	G	A	33	32	19	80	164
Cychrus attenuatus (Fabricius, 1792)	F	R	0	0	0	7	7
Cychrus caraboides (Linnaeus, 1758)	F	A	1	1	3	10	15
Harpalus latus (Linnaeus, 1758)	F	A	0	1	0	0	1
Leistus ferrugineus (Linnaeus, 1758)	G	E	11	0	1	1	13
Leistus piceus Frölich, 1799	F	A	18	6	1	6	31
Notiophilus biguttatus (Fabricius, 1779)	F	A	10	0	0	0	10
Notiophilus palustris (Duftschmid, 1812)	G	E	6	3	1	0	10
Patrobus atrorufus (Stroem, 1768)	G	A	0	1	0	16	17
Pseudoophonus rufipes (De Geer, 1774)	O	E	0	1	0	0	1
Pterostichus aethiops (Panzer, 1797)	F	A	2	1	1	1	5
Pterostichus diligens (Sturm, 1824)	G	A	0	4	8	1	13
Pterostichus niger (Schaller, 1783)	F	E	0	1	1	0	2
Pterostichus oblongopunctatus (Fabricius, 1787)	F	A	8	21	39	12	80
Pterostichus rufitarsis cordatus Letzner, 1842	F	R	6	3	2	6	17
Pterostichus unctulatus (Duftschmid, 1812)	F	A	101	106	73	335	615
Trechus pilisensis sudeticus Pawlowski, 1975	F	A	0	0	2	0	2
Trechus splendens Gemminger et Harold, 1868	F	A	2	15	13	61	91
Trechus striatulus Putzeys, 1847	G	A	8	24	6	198	236
Trichotichnus laevicollis (Duftschmid, 1812)	F	A	13	2	1	21	37
Number of species			23	20	19	20	31
Number of individuals			498	261	228	1717	2704

Beetles were divided into three groups either [a] according to their habitat association: generalist (G), forest (F) and open-habitat (O) species, or [b] according to their ability to cope with environmental changes following Hůrka et al. (1996) as either relicts (R), adaptive (A) or eurytopic (E).