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Recovery of ground-dwelling assemblages during reforestation with native oak depends on the mobility and feeding habits of the species

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ABSTRACT

Timber-oriented forest management causes significant changes to the environments, threaten the survival of many native species and it is responsible for the primary forest loss. Recognition of the scale and effects of the primary forest loss has resulted in a considerable degree of interest in the restoration. One of the serious efforts at restoration is the compulsory reforestation of the clear-felled stands of any (native or non-native) forests with native species. To evaluate the success of restoration efforts it is important to answer whether the diversity and composition of indigenous assemblages can recover after reforestation with native trees and to know how long is the recovery time? We studied ground beetles and millipedes from mature (130-year-old) oak forest, and recently established (5-year-old), young (15-year-old), and middle-aged (45-year-old) reforestation with native English oak by pitfall trapping and leaf litter sifting to assess the recovery dynamics of their diversity and composition. The overall number of the ground beetle individuals and species were significantly the highest in the 5-year-old reforestation, while the overall number of millipede individuals and species were significantly the lowest in the recently established reforestation. The elevated overall number of ground beetle individuals and species in the 5-year-old reforestation were due to the colonization of good disperser open-habitat species. The number of forest-associated ground beetle individuals and species were significantly the lowest in the 5-year-old reforestation, whereas from 15 years after the reforestation, when the canopy has been closing, there was no significant difference in the number of forest species. The number of forest-associated millipede individuals and species were significantly the lowest in the 5-year-old reforestation; however, they were significantly the highest in the natural mature oak forest. Results of both the ordination and the quantitative character species analysis also confirmed that reforestation with native oak after mechanical soil treatment had detrimental effects on both studied ground-dwelling arthropod groups. The diversity and composition of ground beetles with high dispersal ability and less specific feeding habit recovers after the closure of the canopy, while similar recovery do not occur regarding millipedes with low dispersal ability and specific feeding habit. Our results suggest that soil preparation and light tilling should be omitted during the reforestation and cultivation of the reforested stands.

1. Introduction

The worldwide increasing anthropogenic activities cause significant changes to the environments, create patchworks of modified land types and threaten the survival of many native, indigenous species (Kerr and Currie, 1995). One of these harmful human activities is the timber-oriented forest management (Paillet et al., 2010). Almost all native forests in Europe have been altered by anthropogenic activities of varying intensities (Paillet et al., 2010). In Europe 36% of the land surface is forested, however currently 1.7% of the forested area represents natural forests (Parviainen et al., 2000).

In Hungary in the past near 100 years the proportion of the forested areas increased from 11.8% to 22.5%, however, the 75% of the forests are primarily under timber-oriented forest management. Nowadays the natural or natural-like forests consisted of indigenous tree species represent 7.5% of the Hungarian forested area. Pannonic mesophile sand steppe oak forests (*Convallario-Quercetum roboris*) were a prominent feature of the Great Hungarian Plain at the time of European settlement and extended nearly

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the entire lowland. During the last centuries, however a large amount of the original sand steppe oak forests has been lost. In Hungary, the sand steppe oak forests covered approximately 8% of the land surface, however currently they proportion were reduced to 0.2%. The primary cause of sand steppe oak forest loss has been conversion to agricultural production. Additional, significant losses have been caused by overuse and timber production. Moreover, during the reforestation of the clear-felled stands, the fast growing, non-native species (e.g. black locust, red oak, Scots pine) was preferred. Therefore, the sand steppe oak forests have been presently critically endangered forest type in Hungary (Mátyás, 1996).

Recognition of the scale and effects of the loss of sand steppe oak forests in the Great Hungarian Plain has resulted in a considerable degree of interest in their restoration. Serious effort at restoration began in the early 1990s, when, thanks to rigorous Hungarian nature protection legislation in nature protected areas, the area of the clear-cutting has been restricted maximum to 3 hectares. Moreover, in nature protected areas the clear-felled stands of any (native or non-native) forests must been reforested with native species. As a result of the legal regulation, in the nature reserves of the Hungarian Great Plain timber production began the clear-felled stands reforesting with native oak, therefore the area of the reforested English oak (*Quercus robur*) stands is increased.

In a landscape consisting of scattered aged natural sand steppe oak forest stands and several, different aged stands reforested with native English oak, moreover of numerous differently aged non-native plantation a very important research question is immediately emerging. It is important to assess whether the diversity and composition of indigenous ground-dwelling assemblages can recover after reforestation with native oak? Whether the indigenous ground-dwelling species living in the intact, aged natural sand steppe oak forests can colonize the reforested stands and can establish population in these stands? Furthermore, if the diversity and composition of these assemblages recover, how long is the recovery time? Of course recovery of the indigenous ground-dwelling populations in the reforested habitats may depend extremely on the mobility of the species. Species with high dispersal ability can easily colonize the newly created habitats and can establish permanent populations, whereas poor-dispersing species cannot (Guisan and Thuiller, 2005). Other important factor that can significantly determine the success of recolonization and establishing populations is the feeding habit of the species. Species with less specific feeding habit like generalist predators or mixed feeders may find easily their foods in the newly established habitats, than species requiring specific nutriments (e.g. detrivores, Paillet et al., 2010; Toïgo et al., 2013).

We studied the recovery dynamics after reforestation with native oak based on two taxa of ground-dwelling arthropods with contrasting mobility, and being at different trophic level of the food web. Furthermore, multitaxonomic approach is more powerful to assess differential response that could not be detected by single-taxa studies. The family ground beetles (*Coleoptera: Carabidae*) contains more than 40,000 described species. Ground beetles live in nearly every available habitat, although some species are associated with particular ecosystems. Ground beetles are mostly generalist predators and mixed/polyphagous feeders that consume animal (live prey and carrion) and plant material; they are good colonizers via flight or walking (Lövei and Sunderland, 1996). Millipedes (*Myriapoda: Diplopoda*) is the third largest class of terrestrial Arthropoda following Insecta and Arachnida with over 12,000 described species. Millipedes are a major component of terrestrial ecosystems throughout the temperate, subtropical and tropical zones of the world, they occur nearly in all terrestrial environments. Millipedes are ecologically important as detritivores or saprophages (consumers of dead plant material; Golovatch and Kime, 2009). Although dispersal ability is generally considered to be low in millipedes, wandering is widespread in this group. Both ground beetles and millipedes are diverse and abundant, their ecology and systematic are relatively well known, and they seem to be highly sensitive to habitat changes; therefore they are excellent study organisms.

The aim of the present study was to assess the recovery of diversity and composition of ground-dwelling arthropods with different dispersal ability and different feeding habits after reforestation with native oak during a sylvicultural cycle. The cycle represented consecutive, ageing stages in the forestry practice: a native, mature sand steppe oak forest was clear-felled and after mechanical soil treatment was reforested with native English oak. Especially, we tested the following hypotheses: We expected that the diversity of the good-colonizer ground beetles should be the highest in the newly reforested habitats due to the colonization of open-habitat species. Contrary, the diversity of millipedes with low dispersal ability should not be the highest in the youngest reforested stands, because of the depleted colonization. Diversity of the forest specialist ground beetles recovers after the closure of the canopy, while similar pattern do not occur regarding millipedes.

2. Material and methods

2.1. Study area

The study area was located in a large, continuous forested region, in the Nagyerdő Forest Reserve Area at the north-east part of the Great Hungarian Plain near Debrecen city (47°32′N; 21°38′E), the second largest city of Hungary. Pannonic mesophile sand steppe oak forest (*Convallario-Quercetum roboris*) was the dominant forest association in the Nagyerdő Forest Reserve Area. During the last centuries, however a large amount of the original sand steppe oak forests has been clear-felled and reforested. This forestry practice is resulted in a sylvicultural cycle, a chronosequence (a secondary succession). We used a space-for-time substitution procedure to represent the consecutive stages of this sylvicultural cycle: (1) Mature (130-year-old), native Pannonic mesophile sand steppe oak forest, where the English oak (*Q. robur*) was the dominant tree species in the canopy, but field maple (*Acer campestre*) was also present. The shrub and herb layer were moderate. The studied mature stands were not managed for at least 40 years. (2) Recently established, 5-year-old stand reforested with native English oak. It was created after the clear-felling of an aged sand steppe oak forest. After the clear-cutting mechanical soil treatment was applied and the prepared area was put under acorns in equally spaced rows. Spaces between the rows were regularly cultivated by light tilling to prevent weed establishment resulting in open, bare soil surfaces. In the rows weeds, grasses and other species typical of the open habitats were dominant in the dense herb layer, while the shrub layer was moderate. (3) Young, 15-year-old stand reforested with native English oak. The herb and shrub layer were very sparse because of the shading of the closed canopy. Spaces between the rows were occasionally cultivated by light tilling. (4) Middle-aged, 45-year-old stand reforested with native English oak. Due to the closed canopy the herb and shrub layer were moderate. The main habitat characteristics of the stages of the studied sylvicultural cycle estimated around each sampling point are summarized in Table 1. For the spatial replication two stands of each stage of the sylvicultural cycle were investigated. The area of the stands was 3–10 hectares. The average distance between the studied replicates was 499 m (minimum and maximum distances were 400 m and 700 m, respectively). The spatial replicates of a given age class were randomly distributed in the

Table 1
Average values (±S.E.) of the habitat characteristics in the stages of the studied sylvicultural cycle. Average values with different letters indicate a significant ($p < 0.05$) difference by Tukey multiple comparison.

	130-year-old mature	5-year-old reforested	15-year-old reforested	45-year-old reforested
Cover of leaf litter (%)	81.8 ± 2.83^{a}	19.5 ± 1.62^{b}	85.7 ± 2.01^{ac}	91.9 ± 1.37^{c}
Cover of decaying wood materials (%)	9.3 ± 0.86^{a}	0.5 ± 0.06^{b}	5.2 ± 0.28^{c}	8.1 ± 0.54^{a}
Cover of herbs (%)	19.1 ± 2.81^{a}	32.1 ± 3.20^{b}	7.2 ± 1.69^{c}	12.0 ± 1.09^{ac}
Cover of shrubs (%)	54.8 ± 3.54^{a}	37.6 ± 1.86^{b}	1.2 ± 0.73^{c}	35.2 ± 4.61^{b}
Canopy cover (%)	65.6 ± 3.77^{a}	0.0 ± 0.00^{b}	84.3 ± 2.22^{c}	76.3 ± 2.79^{c}

study area, thus not forming age-specific aggregates. The soil type in the studied stands was identical, sandy soil with humus.

2.2. Sampling design

Sampling of the ground-dwelling arthropods carried out with the most commonly used method for the studied taxon. Ground beetles were collected by unbaited pitfall traps. Traps consisted of 100 mm diameter plastic cups (volume 500 ml) and contained about 200 ml 70% ethylene glycol as a killing-preserving solution and a little detergent to break the surface tension of the liquid. Pitfall traps were protected by fiberboard from litter and rain. There were 12 randomly placed traps in all studied stands. This resulted in a total of 96 traps (4 stands $\times$ 2 replicates $\times$ 12 traps). Each trap was at least 30 m from the forest edges, in order to avoid edge effects (Magura, 2002; Tóthmérész et al., 2014). Traps were 15–25 m apart from each other to provide statistically independent samples and true replicates (Digweed et al., 1995). The average distance between the traps was 20 m, while the minimum and maximum distance between the traps was 15 and 25 m, respectively. Trapped beetles were collected three-weekly from April to October in 2011. Ground beetles were identified to species level using standard keys (Hůrka, 1996). Nomenclature follows also Hůrka (1996). For the numerical analyses we pooled samples of a trap from different sampling periods.

For sampling arthropods which are active in litter and debris the leaf litter sifter is the most commonly used method. Therefore, millipedes were collected at each stands using leaf litter sifter. The litter samples were collected with a frame of sifter ($25 \times 25 \times 5$ cm). Litter and debris were sifted vigorously and stored in a bag which was sealed. Millipedes were extracted manually from each sample in the laboratory, and the materials were preserved in 70% alcohol. There were 5 randomly placed litter sampling points in each stand. This resulted in a total of 40 samples (4 stands $\times$ 2 replicates $\times$ 5 samples). Similarly to the spatial arrangement of pitfall traps, each litter sample was at least 30 m from the forest edges and they were also 15–25 m apart from each. Litter samples were collected three-weekly from April to October in 2011. All millipedes taken in litter samples were identified to species level using standard keys (Hauser and Voigtländer, 2009). Nomenclature follows Enghoff (2013). For statistical analyses litter samples were also pooled for the whole year.

2.3. Data analyses

Habitat affinity (forest or open-habitat species) and dispersal ability of the collected species was designated from the literature for both the ground beetles (Hůrka, 1996) and the millipedes (Hauser and Voigtländer, 2009; Wytwer et al., 2009; Voigtländer, 2011). Macropter ground beetles observed in flight and millipedes with moderate dispersal ability were regarded as good dispersers. Generalized Linear Mixed Models (GLMs) were used to test differences in the overall number of individuals and species, the number of the ground beetle and millipede individuals and species with different habitat affinity, and in the number of good disperser ground beetle and millipede individuals and species among the four forest types (native, mature sand steppe oak forest, 5-year-old, 15-year-old and 45-year-old reforestations with English oak). In the model the factorial design was applied, where the stages of the sylvicultural cycle (age classes) and the spatial replicates were used as categorical variables. We used data from the individual traps or litter samples. The response variable (number of individuals and species richness) was defined as following a Poisson distribution (with log link function). The Poisson distribution assumes that the mean and variance are equal. Real data do not follow this, and the variance is often larger than the mean. This biological reality (overdispersion) was also incorporated into the model using the Pearson Chi^2 (quasi-Poisson distribution). That is, GLMs based on quasi-Poisson distribution were used (Zuur et al., 2009). When the overall GLMs revealed a significant difference between the means, a Tukey test was performed for multiple comparisons among means.

Composition of ground beetle and millipede assemblages in the forest types was compared at sample (trap or litter sample) level using multidimensional scaling (MDS) based on abundance data using the Hellinger distance (also known as Bhattacharyya distance; Legendre and Legendre, 1998). The characteristic species for the stages of the studied sylvicultural cycle (for the mature sand steppe oak forest, the 5-year-old, the 15-year-old and the 45-year-old reforestations) was explored by the IndVal (Indicator Value) procedure (Dufrêne and Legendre, 1997). It is a useful method to find indicator species and/or species assemblages characterizing groups of samples. The novelty of this approach, compared to the other indicator species analyses, lies in the way that it combines a species' abundance with its frequency of occurrence in the various groups of samples. Indicator species are defined as the most characteristic species of each group, found mostly in a single group and present in the majority of sites belonging to that group. The method derives indicators from any hierarchical or non-hierarchical site classification. The indicator value is maximum (100) when all individuals of a species are found in a single group of sites (high specificity) and when the species occurs in all sites of that group (high fidelity). The statistical significance of the species indicator values is evaluated by a Monte-Carlo reallocation procedure. The significance is evaluated by the comparison of the observed values to the values obtained from the random Monte-Carlo permutations. The IndVal method is robust to differences in the numbers of sites between site groups, to differences in abundance between sites within a particular group, and to differences in the absolute abundances of different species or taxa. The IndVal method is a quantitative characterization of the idea of indicator species; thus it would be better to mention the indicator species as quantitative character species (Elek et al., 2001).

3. Results

Altogether 7258 ground beetle individuals belonging to 70 species were trapped during the study. This included 725 individuals from 40 species in the mature sand steppe oak forest, 4345 individuals of 46 species in the 5-year-old reforestation, 796 individuals of 34 species in the 15-year-old reforested stands, while 1392 individuals from 34 species in the 45-year-old reforestation. The most numerous species was *Harpalus flavescens*, a macropter species; 1926 individuals (comprising 26.5% of the total catch) were trapped exclusively in the 5-year-old reforestation (Appendix). A total of 1016 millipede individuals belonging to 9 species were collected by litter sifter. In the native sand steppe oak forest 448 individuals from 7 species were caught, in the 5-year-old reforestation 14 individuals of 1 species were captured, in the 15-year-old reforested stands 285 individuals of 8 species were collected, while in the 45-year-old reforestation 269 individuals from 8 species were sampled. The most numerous species was *Megaphyllum projectum*, 372 individuals (36.65% of the total catch) were collected (Appendix).

The overall number of ground beetle individuals and species were significantly higher in the 5-year-old reforestation than in the other forest types ($\chi^2 = 154.25$; d.f. = 3, 3; $p < 0.0001$ and $\chi^2 = 60.85$; d.f. = 3, 3; $p < 0.0001$, respectively; Fig. 1). The average number of individuals was almost six times, while the average number of ground beetle species was more than one-and-a-half times higher in the 5-year-old stands compared to the mature stands (Fig. 1). An opposite trend was observed for the overall number of millipede individuals and species, as they were significantly lower in the 5-year-old reforestation than in the other stages ($\chi^2 = 41.86$; d.f. = 3, 3; $p < 0.0001$ and $\chi^2 = 188.38$; d.f. = 3, 3; $p < 0.0001$, respectively; Fig. 1). In the 5-year-old stands the average number of millipede individuals was fallen by one-thirtieth, and the number of species decreased by a quarter compared to the mature forest stands (Fig. 1). The number of forest-associated ground beetle individuals and species were significantly lower in the 5-year-old reforestation ($\chi^2 = 62.64$; d.f. = 3, 3; $p < 0.0001$ and $\chi^2 = 66.53$; d.f. = 3, 3; $p < 0.0001$, respectively; Fig. 2). There was no significant difference in the number of forest species when the canopy has been closing (from 15 years after the reforestation, Fig. 2). In the 5-year-old stands the average number of ground beetle individuals and species were more than one third lower than in the mature stands (Fig. 2). The number of forest-associated millipede individuals and species were significantly the lowest in the 5-year-old reforestation, however they were significantly the highest in the mature sand steppe oak forest, and there were no significant difference in these variables between the 15-year-old and the 45-year-old reforestations ($\chi^2 = 231.20$; d.f. = 2, 2; $p < 0.0001$ and $\chi^2 = 309.24$; d.f. = 2, 2; $p < 0.0001$, respectively; Fig. 2). In the 5-year-old stands all of the forest-associated millipedes were lost (Fig. 2). The number of open-habitat ground beetle individuals and species were significantly higher in the 5-year-old reforestation compared to the other forest types ($\chi^2 = 49.83$; d.f. = 3, 3; $p < 0.0001$ and $\chi^2 = 222.81$; d.f. = 3, 3; $p < 0.0001$, respectively; Fig. 3). The number of open-habitat millipede individuals and species were also significantly different among the studied stands ($\chi^2 = 16.91$; d.f. = 3, 3; $p = 0.0007$ and $\chi^2 = 13.83$; d.f. = 3, 3; $p = 0.0031$, respectively; Fig. 3). The number of open-habitat millipede species was significantly the lowest in the mature stands. In the 5-year-old stands the average number of open-habitat ground beetle individuals was more than two hundred and fifty times higher, while the average number of species was twenty times higher than in the mature stands. The average number of open-habitat millipede individuals was one-third lower, while the average number of open-habitat species was two and a half times higher in the 5-year-old stands than in the mature ones (Fig. 3). The number of good disperser (macropter and observed in flight) ground beetle individuals and species were significantly the highest in the 5-year-old reforestation ($\chi^2 = 108.29$; d.f. = 3, 3; $p < 0.0001$ and $\chi^2 = 112.44$; d.f. = 3, 3; $p < 0.0001$, respectively; Fig. 4). The number of good disperser millipede individuals and species were significantly the lowest in the 5-year-old reforestation ($\chi^2 = 43.74$; d.f. = 3, 3; $p < 0.0001$ and $\chi^2 = 114.91$; d.f. = 3, 3; $p < 0.0001$, respectively; Fig. 4).

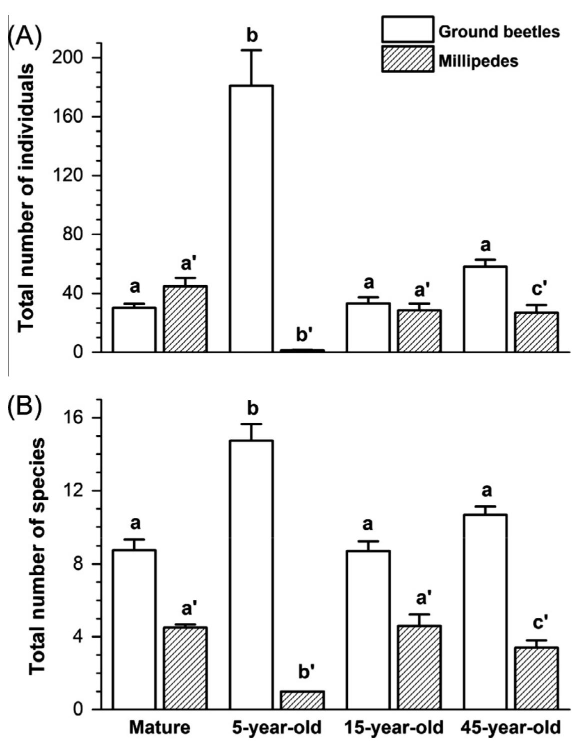

Fig. 1. Mean total number of ground beetle and millipede (A) individuals and (B) species (±SE) in the stages of the sylvicultural cycle. Different letters indicate significant differences by Tukey test ($p < 0.05$); normal letters denote test for ground beetles, and letters with apostrophe denote test for millipedes.

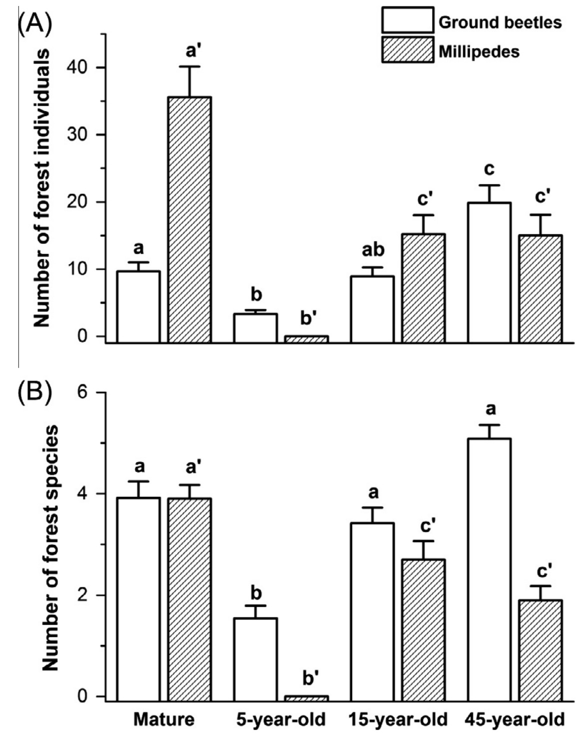

Fig. 2. Mean number of forest-associated ground beetle and millipede (A) individuals and (B) species (±SE) in the stages of the sylvicultural cycle. Different letters indicate significant differences by Tukey test ($p < 0.05$); normal letters denote test for ground beetles, and letters with apostrophe denote test for millipedes.

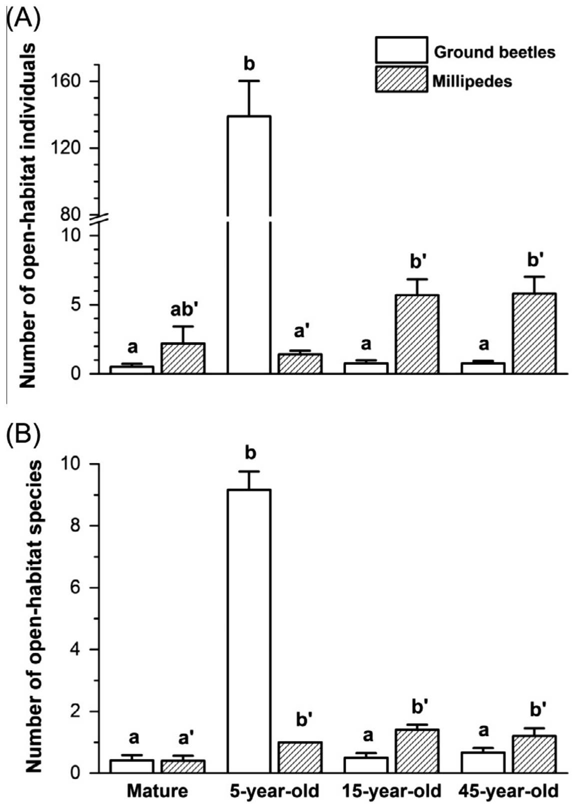

Fig. 3. Mean number of open-habitat ground beetle and millipede (A) individuals and (B) species (±SE) in the stages of the sylvicultural cycle. Different letters indicate significant differences by Tukey test ($p < 0.05$); normal letters denote test for ground beetles, and letters with apostrophe denote test for millipedes.

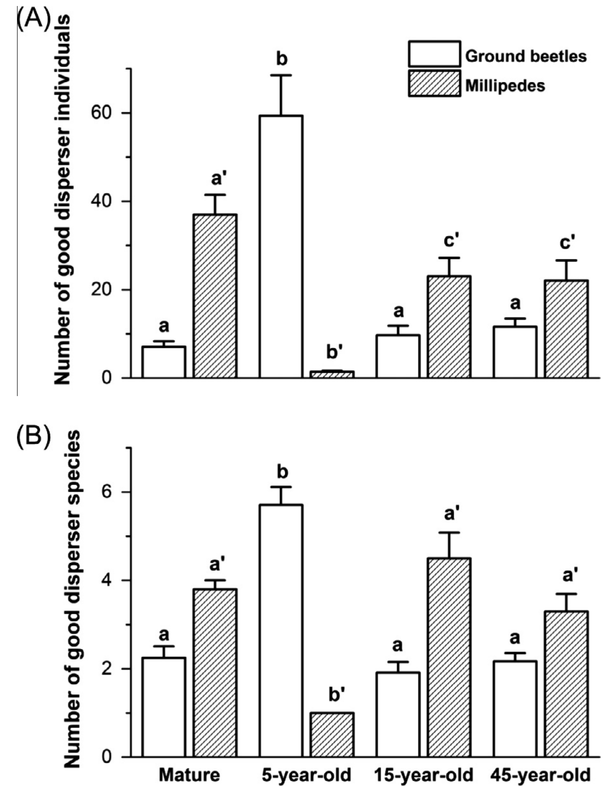

Fig. 4. Mean number of good disperser ground beetle and millipede (A) individuals and (B) species (±SE) in the stages of the sylvicultural cycle. Different letters indicate significant differences by Tukey test ($p < 0.05$); normal letters denote test for ground beetles, and letters with apostrophe denote test for millipedes.

The ground beetle assemblages of the 5-year-old reforestation were strongly separated from the assemblages of the other forest types along the first ordination axis, while the composition of the ground beetle assemblages of the mature sand steppe oak forest, the 15-year-old reforestation and the 45-year-old reforestation were very similar to each other (Fig. 5a). Samples from the 5-year-old reforestation separated explicitly from the other samples based on the composition of the millipede assemblages along the first ordination axis, nevertheless the composition of samples of the 5-year-old reforestation were very similar to each other, as these samples consisted only of one millipede species. Furthermore, samples of the mature sand steppe oak forest, the 15-year-old reforestation and the 45-year-old reforestation formed rather distinct group in the ordination space (Fig. 5b).

Based on the result of the multivariate analysis we defined five groups of significant quantitative character ground beetle species by the IndVal analysis (Fig. 6a): (1) species that were trapped exclusively or were the most abundant in the mature sand steppe oak forest (*Synuchus vivalis*, *Ophonus nitidulus*); (2) species that were recorded exclusively or were found numerously in the 5-year-old reforestation (*H. flavescens*, *Pseudoophonus griseus*, *Calathus erratus*, *Pseudoophonus rufipes*, *Harpalus distinguendus*); (3) species preferring the forests with closed canopy (mature sand steppe oak forest, 15-year-old and 45-year-old reforestations; *Carabus violaceus*, *Pterostichus niger*, *Pterostichus oblongopunctatus*, *Amara convexior*); (4) species that were the most abundant in the mature sand steppe oak forest and the 45-year-old reforestation (*Carabus granulatus*, *Pterostichus melas*); and (5) species that were recorded exclusively in the 45-year-old reforestation (*Harpalus xanthopus winkleri*). Regarding millipedes only three groups of significant quantitative character species can be classified by the IndVal method (Fig. 6b):

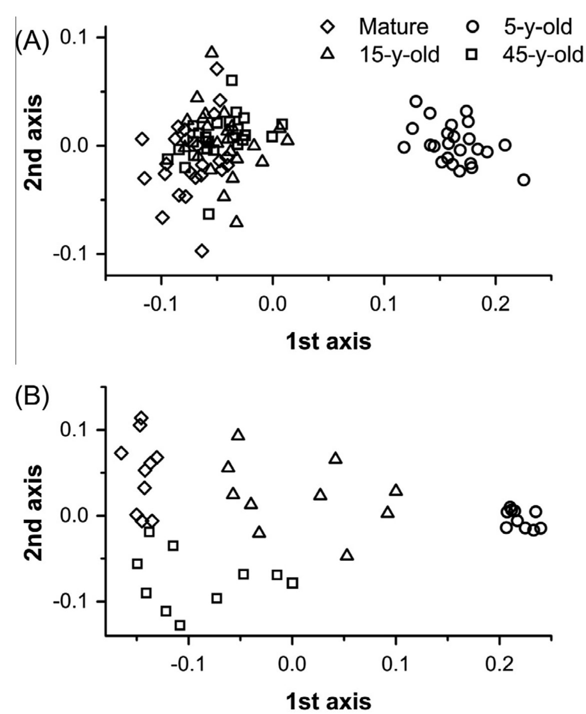

Fig. 5. Ordination (multidimensional scaling using the Hellinger distance) of the ground beetle (A) and the millipede (B) assemblages for the sylvicultural cycle.

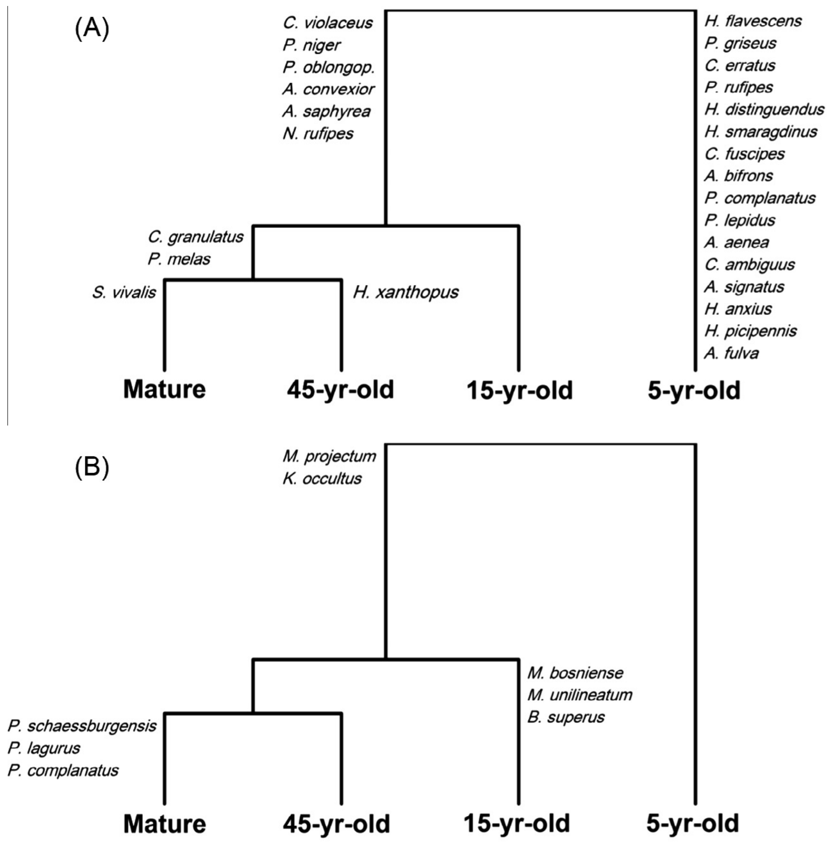

Fig. 6. Significant quantitative character ground beetle (A) and millipede (B) species for the forest stands identified by the IndVal method. Only species with 25 or higher indicator value are shown.

(1) species preferring the mature sand steppe oak forest (*Polydesmus schaessburgensis*, *Polyxenus lagurus*, *Polydesmus complanatus*); (2) species that were sampled exclusively in the forests with closed canopy (mature sand steppe oak forest, 15-year-old and 45-year-old reforestations; *Megaphyllum projectum*, *Kryphioiulus occultus*); and (3) species that were the most abundant in the 15-year-old reforestation (*Mastigona bosniense*, *Megaphyllum unilineatum*, *Brachydesmus superus*).

4. Discussion

4.1. Responses of ground beetles to reforestation

Almost all studies have documented pronounced changes in ground beetle assemblages after clear-cut originated drastic habitat alterations (for review, see Koivula, 2011). Responses of ground beetles to clear-cut harvesting are most markedly detectable in the early phase, within 1–3 years after the clear-felling (Szyszko, 1983; Niemelä et al., 2007; Koivula, 2011; Schwerk and Szyszko, 2011). However, the direction of the change in carabid diversity in the early phase of clear-cut originated reforestation is rather different. Elevated ground beetle abundance and/or diversity (even twice as much) was found in the youngest stages of the clear-cut originated natural forest regeneration both in Europe (Koivula et al., 2002) and North America (Buddle et al., 2006). Studying regenerating native young stands, which were lightly prepared after the clear-cutting (scarified and partly planted with native saplings), similar abundance and diversity pattern was observed (Niemelä et al., 1993; Pohl et al., 2007). These youngest stages were invaded by open-habitat and habitat generalist species, moreover some closed-forest specialist ground beetle species were also survived, contributing to the elevated diversity (Niemelä et al., 1993; Koivula et al., 2002; Buddle et al., 2006). At the youngest stages of non-native plantations established after clear-cutting of native forest stands without site preparation increased ground beetle abundance and/or species richness (even more than one-and-a-half times increase) was reported due to the invasion of open-habitat and generalist species, and the persistence of some closed-forest specialist species (Butterfield, 1997; Huber and Baumgarten, 2005; Taboada et al., 2008). However, heavy site preparation after the clear-cutting (e.g. grubbing, tilling, deep loosening, burning) is accompanied by lower ground beetle abundance and/or diversity in the youngest stands (abundance may decrease five- to tenfold, while species richness loss may reach 60%) both in deciduous (Yu et al., 2006) and coniferous non-native plantations (Magura et al., 2003). Open-habitat and habitat generalist ground beetle species can easily colonize these heavily prepared sites. However, the preparation eliminates microhabitats required by the forest specialist species causing complete destruction of these species from the prepared youngest stands (Magura et al., 2003). Disappearance of forest specialist species and invasion of open-habitat and habitat generalist species may cumulate lower diversity in the prepared youngest stands. Of course, regional species pool is an other relevant factor shaping local diversity of ground beetles (Koivula, 2011). Namely, the abundance and diversity of ground beetles in the heavily prepared young stands are extremely depending on the species pool of the matrix. At the young stands embedded in a matrix with vast amount of open-habitat and habitat generalist species, the rapid and expansive colonization of these species can easily result in an elevated ground beetle abundance and diversity. In our present study we found elevated average abundance and species richness of ground beetles in the youngest, 5-year-old native deciduous broad-leaved reforestation (almost four time gain in abundance and one-and-a-half times gain in species richness), because of the extreme invasion of good disperser open-habitat and generalist species, which accounted about 90% of the species pool.

Results concerning diversity and composition of ground beetle assemblages in later phases of clear-cut originated reforestations are rather consistent (for review, see Koivula, 2011). Studies illustrated that, despite the different carabid species pool of the various regions, the general patterns of their responses to the clear-cut originated habitat alterations were very similar (Niemelä et al., 2007). Namely, the early, open phases of forest secondary succession are characterized by a different set of species than are the later phases with a closed tree canopy (Niemelä et al., 1993, 2007; Elek et al., 2001; Magura et al., 2002, 2003, 2006; Pohl et al., 2007; Koivula, 2011; Lange et al., 2014). Clear-cutting results in open-area and promotes the colonization and survival of open-habitat and succession-generalist (habitat generalist) species, while these changes in habitat structure and microclimatic conditions reduce the survival of closed-forest specialist ground beetles (Szyszko, 1983; Szujecki et al., 1983; Koivula, 2002; Pawson et al., 2011; Toivanen et al., 2014). After canopy closure the number of the open-habitat and habitat generalist species begins to decline drastically, while forest specialist species begin to recover. Elek et al. (2005) found that closure of the canopy between 6 and 8 years after the planting, strongly facilitated the recolonization of forest carabid species in Norway spruce stands of north Hungary. Studying beetles in extensive *Pinus radiata* plantations with different age in New Zealand, Pawson et al. (2011) also concluded that recovery time was closely linked to the development of a closed canopy (8–16 years after the planting), with distinct differences in the responses of individual species reflecting habitat preferences for open or closed forest stands. Similarly, in Finnish spruce forests carabid assemblages changed remarkably during the first 20–30 years following clear-cutting, but not much after that, as samples from older forests were relatively similar (Koivula et al., 2002). In aspen-dominated forest stands originating from clear-cutting litter-dwelling arthropod assemblages (ground beetles, rove beetles and spiders) also showed partial recovery after 30 years of the harvesting, as the assemblages from old and mature stands were similar in species composition (Buddle et al., 2006). Taboada et al. (2008) also reported that canopy cover development strongly influenced the ground beetle assemblages resulting in more similar assemblages at forested stages of the ageing sequence. Our results also suggested that the diversity and composition of ground beetles were not notably different after the canopy closing, which occurred after 15 years of the reforestation. The relatively fast recovery of the diversity and composition of ground beetles was probably due to the ecological flexibility of several forest species, the high dispersal ability and less specific feeding habit. Environmental conditions (e.g. amount of leaf litter, herbs, moisture, microclimate) in forest stands with closed tree canopy are something similar, so the forest generalist species and the majority of the forest specialist species can find their preferred habitat requirements in these stands due to their ecological flexibility. Carabids with flight ability cover long distances, however still the flightless carabids move up to some hundreds of meters by foot (Lövei and Sunderland, 1996), so they can simply colonize the forest stands with closed tree canopy from the neighboring mature stands. Ground beetles have an opportunistic feeding habit and are mostly polyphagous feeders that consume animal (live prey and carrion) and plant material (Lövei and Sunderland, 1996). After the canopy closure the food spectrum and supply for ground beetles may be similar, therefore the forest-associated species can find easily their foods in the closed forest stands with similar environmental conditions. Toïgo et al. (2013) also showed that basal area and humus activity, respectively proxies for canopy closure and food supply, increased the total species richness, and the richness of forest and carnivorous species.

In the present study there were no significant differences in both the overall ground beetle abundance and species number and the number of forest-associated ground beetle species among the forest stages with closed tree canopy (the mature sand steppe oak forest, the 15-year-old and the 45-year-old reforestations), in addition the composition of the ground beetle assemblages of these closed forest stands was very similar. However, by the IndVal (Indicator Value) procedure we identified several ground beetle species that were trapped exclusively or were the most abundant in the mature sand steppe oak forest. Pohl et al. (2007) suggested that stand age is a key determinant of the ground beetle assemblage. However, they showed that the beetle assemblages of the regenerating stands from 1 to 27 years post-harvest became more similar to the assemblages of the mature stands as they aged, but still differed considerably from them yet 27 years after the clear-cutting. Similarly, several studies reported that some forest specialist carabid species are unable to recover from clear-cutting during the forest secondary succession (Skłodowski, 2006; Niemelä et al., 2007; Pohl et al., 2007). Habitat preferences or dispersal limitations may prevent the recolonization of these stenotopic forest ground beetle species in the reforested stands (Niemelä et al., 1993; Magura et al., 2003; Pohl et al., 2007). Such specialist species with poor dispersal ability require microsites defined by abiotic and biotic conditions (e.g. shady and moist sites, coarse woody debris, decaying wood material) as it was previously emphasized (Desender et al., 1999; Toïgo et al., 2013; Skłodowski, 2014a; Negro et al., 2014). These conditions are more commonly met in mature stands than in clear-cuts or young and middle-aged closed stands. Soil preparation before the reforestation (mechanical soil treatment) and the cultivation by light tilling during the management of the reforested stands eliminate the microsites required by the specialist species, and have strong effects on specialist carabids and their recovery (Skłodowski, 2014b). The recovery of stenotopic forest carabids may take hundreds of years if the soil is strongly altered during the forest management and if large-scale logging is practiced (Desender et al., 1999). The importance of the microsites, microhabitat characteristics in the survival and recovery of specialist species have reported by several studies on other beetle taxon, too (e.g. for saproxylic beetles: McGeoch et al., 2007; Stenbacka et al., 2010).

4.2. Responses of millipedes to reforestation

In contrast to ground beetles data on millipedes over the run of secondary forest succession are rather scarce (but see Szujecki et al., 1983; Schreiner et al., 2012). Comparing differently aged (from 10-year-old to 95-year-old) Norway spruce monocultures, Purchart et al. (2013) found no difference in the number of millipede individuals and species among the succession stages. Similarly, in a managed beechwood chronosequence (28–197 years old) the total abundance and species richness of detritivore macro-invertebrates (lumbricids, isopods and diplopods) were similar in the stages (Hedde et al., 2007). However, samples from the youngest stages (1–5-year-old) were missing in the above studies, therefore the exhaustive comparison along the chronosequence is impossible. Other studies showed that the species richness of millipedes was higher (almost twofold) in the aged stands than in the younger phases of the succession. Reanalyzing millipedes data of Schreiner et al. (2012) from differently aged (1–165-year-old) beech forests in Western Germany, the yearly mean number of species showed a marginally significant increase with the ageing of the stands ($R = 0.51$; $F = 4.13$; d.f. = 1, 13; $p = 0.06$); similar trend was not observed regarding the yearly mean number of millipede individuals ($R = 0.25$; $F = 0.79$; d.f. = 1, 13; $p = 0.39$). Studying millipedes in three successional stages of alluvial hardwood forest (3-, 30- and 80-year-old *Querco-Ulmetum* stands) along the Morave River in the Czech Republic Tuf and Ožanová (1999) showed that the number of millipede individuals and species were the lowest (only a one half) in the youngest stands and it increased towards ageing.

We demonstrated that clear-cutting and reforestation with native oak after soil preparation had detrimental effects on the millipede assemblages, as in the 5-year-old stands the average number of millipede individuals was fallen by one-thirtieth, and the number of species decreased by a quarter compared to the mature forest stands. Our results contradict the hypothesis of Ponge et al. (1998) which predicts community changes during natural forest regeneration, a shift from soil-dwelling-dominated community in young and mature stands (heterotrophic phase: transformation of moder humus to mull, thus mineralization exceeds photosynthesis) towards litter-dweller-dominated communities in regeneration, middle-aged stands (autotrophic phase: the growth of trees is characterized by carbon accumulation, increased uptake of nutrients, and the development of moder humus in the topsoil, thus photosynthesis exceeds mineralization). In fact, the species richness and abundance of litter-dwelling millipedes were significantly lower in the young, 5-year-old reforestations, conversely to the hypothesized increase of litter-dwelling detritivore density and biomass in the young stands (Ponge et al., 1998). Moreover, the millipede species richness and abundance were not significantly different in the mature and regenerating (15-year-old) stands, again underlying the discrepancy from the hypothesis of Ponge et al. (1998). The main reason for the difference between our results and the above mentioned hypothesis lies in the fact that the soil preparation before the reforestation and the cultivation by light tilling during the management may drastically alter the nutrient cycling and the mineralization processes of the reforested stands.

In the present study the number of millipede individuals and species were similar in the forest stands with closed tree canopy (15-, 45-year-old and mature stands). This result may suggest that the drastically altered millipede assemblages by clear-cutting recover after 15 years of the reforestation. However, analyzing the number of forest-associated millipede individuals and species it is evident that millipedes do not recover at all, as the number of forest-associated species and their abundance were significantly higher in the mature stands compared to the young and middle-aged (15- and 45-year-old) reforested stands. Results concerning the composition of millipede assemblages also highlight that millipedes do not recover with the ageing of reforested stands, since samples from the studied forest stands form distinct groups in the ordination space. Even the number of good disperser millipede individuals was significantly lower in the 5-, 15- and 45-year-old stands than in the mature stands. Analysis of the quantitative character species (IndVal procedure) also showed that there are millipede species characteristic to the mature stands, and these forest specialist species are missing from the recently established (5-year-old) stands, moreover the abundance of these species is considerably lower in the young (15-year-old) and middle-aged (45-year-old) stands than in the mature stands. Nearly fifty years after reforestation several forest specialist millipede species have yet significantly lower abundance in the middle-aged (45-year-old) stands compared to the mature stands. These results can not be compared with other published ones, because to our knowledge this study is the single one that examined the changes in the number of forest-associated millipede species along a clear-cut originated reforestation. Nevertheless, the delayed recovery regarding millipedes may be attributed to the fact that the age gradient (from 5 to 45 years after clear-cutting) considered in the present study was not complete and the recovery of millipedes with lower dispersal abilities may be longer (more than 45 years).

Several factors influence the spatial distribution of millipedes both on a broad scale and on the smaller scale. The most important edaphic factors are soil temperature, soil mineral content (especially calcium and magnesium), soil humidity, soil pH and humus profile and type (Hopkin and Read, 1992; Stašiov, 2009). Relevant other environmental factors are the amount of litter and coarse woody debris, the canopy cover and the microclimate (Jabin et al., 2004; Hättenschwiler et al., 2005; Purchart et al., 2013). Of course, food and microhabitat preferences and resistance to desiccation or waterlogging are also key factors (David and Handa, 2010; Snyder et al., 2013). Previous publications underlined the significant impact of the presence of litter and coarse woody debris on the spatial pattern, composition, density and diversity of millipedes (Szujecki et al., 1983; Topp et al., 2006; Kappes et al., 2007; Purchart et al., 2013). Coarse woody debris (branches, logs and stumps on the forest floor) offers sheltered micro-habitats, food sources and breeding sites for ground dwelling arthropods. The clear-cutting, the soil preparation before reforestation and the cultivation by tilling during the management of the reforested stands significantly alter the edaphic and environmental conditions and eliminate the microhabitats required by the millipedes. Furthermore, millipedes have rather limited dispersal power. Dispersal by walking is the main spreading mechanism of millipedes, although dispersal by wind for small species occurs occasionally (Hopkin and Read, 1992). However, millipedes generally need a rather long time for site immigration (Dunger and Voigtländer, 2009). In our study the cover of leaf litter and decaying wood materials, which were proven important microhabitats for millipedes, were similar in the 45-year-old reforestation and in the mature stands. Thus, in these forest stands the microhabitats may be considered as roughly equivalent for millipedes. However, despite the comparable amount of microhabitats, the number of forest-associated millipede individuals and species were still significantly higher in the mature stands compared to the middle-aged (45-year-old) reforested stands, again proving the delayed recovery of millipedes. The above discussed, complex and interacting factors play important role in the failing of recovery of millipede assemblages after clear-cut originated secondary forest succession demonstrated in the present study.

The impoverishment and the changes in composition of millipede assemblages may have vital effect on the ecosystem processes and ecosystem services as well (Lavelle et al., 2006). Soil detritivore macro-invertebrates have a high functional importance in the ecosystem processes; moreover they play principal roles in several ecosystem services such as organic matter decomposition, water cycling or primary productivity. In forest ecosystems, soil detritivores participate in the comminution of fresh dead leaves, the stimulation of microbial activities, thus in the organic matter mineralization. As soil invertebrates are highly sensitive to disturbances, the modification of their habitats may significantly decrease their activity and diversity, leading even to soil dysfunctioning and ecosystem degradation (Lavelle et al., 2006).

5. Conclusion

Our study showed that ground beetles and millipedes responded differently to the reforestation with native oak after soil preparation and cultivation by light tilling during the management. The diversity and composition of ground beetles with high dispersal ability and less specific feeding habit recovers after the closure of the canopy, while similar recovery do not occur regarding millipedes with low dispersal ability and specific feeding habit. The age gradient considered in the present study was not complete, therefore further studies are probably needed to get an improved estimation of the recovery time for species. Based on our results we recommend that soil preparation and light tilling should be omitted during the reforestation and cultivation of the reforested stands. Treatments that do not alter the edaphic and environmental conditions in the reforested stands and do not eliminate the microhabitats required by the specialist species could be proposed during the forest management.

Even-aged (modified clear-cutting, seed tree method and shelterwood harvesting) and uneven-aged regeneration methods (group selection and single tree selection) could be less intensive and harmful sylvicultural practices than the conventional clear-fell harvest model with soil preparation. Modified clear-cutting with protection of the advanced growth and soils had already less harmful impact on biodiversity within managed forests (Légaré et al., 2011). During the (uniform or grouped or irregular) green-tree retention treatments trees left after cutting either to provide seeds for natural regeneration (seed tree method) or to produce shaded or partially-shaded microenvironment for seedlings (shelterwood cutting). Residual green-tree patches may preserve some of the heterogeneity, structural features and environmental conditions required by the forest specialist species (Pinzon et al., 2012), therefore they may function as important refuges for forest specialist invertebrates (Matveinen-Huju et al., 2006) and thereby contribute to maintaining forest biodiversity (Rosenvald and Lõhmus, 2008). Group selection and single (individual) tree selection methods harvest and remove some trees in most size classes either singly, in small groups, or in strips, contributing to establish and grow multi-aged stand. The uneven-aged management methods based on selection have become more popular in the European heterogeneous forest landscapes (Redon et al., 2014). Recent studies indicate that uneven-aged management methods using selection cuttings maintain mature or late-successional forest characteristics and species assemblages better than even-aged management methods (Siira-Pietikäinen and Haimi, 2009; Kuuluvainen et al., 2012).

Besides the sylvicultural methods the patterns and processes at landscape level are also very important during the forest management. Since forest specialist species are threatened by fragmentation and habitat loss, therefore to ensure their survival it is important the appropriate proportion of the uncut, mature stands and the regenerating stands in forest systems (Pohl et al., 2007). At the landscape level the large-scale harvesting of mature stands and the emergence of numerous clear-felled sites make more difficult or at worst hamper the recolonization of regenerating stands by forest specialist species. Destruction of mature stands causes a direct extinction of forest specialist species abolishing the recolonists, while clear-felled sites are impenetrable barriers for these specialist species contributing to the isolation of the remnant mature stands (Magura et al., 2000). We conclude that maintaining forest specialist species and biodiversity in sylvicultural systems, mature forest stands should be large and connected to other stands (Pohl et al., 2007).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.12.015.

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