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Corresponding Author	Family Name	**Nagy**
	Particle	
	Given Name	**Dávid D.**
	Suffix	
	Division	
	Organization	MTA-DE Biodiversity and Ecosystem Services Research Group
	Address	Egyetem tér 1, Debrecen, 4032, Hungary
	Email	david.nagy111@gmail.com
Author	Family Name	**Magura**
	Particle	
	Given Name	**Tibor**
	Suffix	
	Division	Department of Ecology
	Organization	University of Debrecen
	Address	P.O. Box 71, Debrecen, 4010, Hungary
	Email	
Author	Family Name	**Debnár**
	Particle	
	Given Name	**Zsuzsanna**
	Suffix	
	Division	
	Organization	MTA-DE Biodiversity and Ecosystem Services Research Group
	Address	Egyetem tér 1, Debrecen, 4032, Hungary
	Email	
Author	Family Name	**Horváth**
	Particle	
	Given Name	**Roland**
	Suffix	
	Division	Department of Ecology
	Organization	University of Debrecen
	Address	P.O. Box 71, Debrecen, 4010, Hungary
	Email	
Author	Family Name	**Tóthmérész**
	Particle	
	Given Name	**Béla**

Suffix	
Division	
Organization	MTA-DE Biodiversity and Ecosystem Services Research Group
Address	Egyetem tér 1, Debrecen, 4032, Hungary
Email	

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Abstract

Creating plantations after clear-cutting of native forests is a serious risk for biodiversity. Rove beetles were collected by litter sifting in non-native plantations (black locust, Scots pine, red oak), in native oak plantation and mature oak forest as control. We hypothesised that diversity and composition of the rove beetles in the mature forest would be different from those in the plantations. We expected that reforestation with native species would have less harmful effects on rove beetles than reforestation with non-native species. In accordance with our hypotheses the overall number of rove beetle individuals and species, as well as the diversity of hygrophilous and decaying material dependent rove beetles were significantly lower in the plantations than in the mature oak forest. However, the overall species richness and the diversity of hygrophilous and decaying material dependent rove beetles were significantly higher in the native plantation compared to the non-native ones. There was no significant correlation between the diversity of these rove beetles and the soil moisture and decaying woody materials as limiting resources; thus, our study did not support the resource quantity hypothesis. The cover of herbs and shrubs, the soil temperature and soil pH were the most important factors controlling the diversity of rove beetles. Our results suggest that reforestation with native tree species provides more suitable habitat for rove beetles than non-native ones. However, it seems that rove beetle assemblages did not recover even after 40 years of reforestation with native tree species due to their specific ecological demands.

Keywords (separated by '-')	Diversity - Hygrophilous species - Mature oak forest - Native plantation - Non-native plantations - Resource quantity hypothesis

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ORIGINAL PAPER

Shift of rove beetle assemblages in reforestations: Does nativity matter?

Dávid D. Nagy[1] · **Tibor Magura**[2] · **Zsuzsanna Debnár**[1] · **Roland Horváth**[2] · **Béla Tóthmérész**[1]

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Abstract Creating plantations after clear-cutting of native forests is a serious risk for biodiversity. Rove beetles were collected by litter sifting in non-native plantations (black locust, Scots pine, red oak), in native oak plantation and mature oak forest as control. We hypothesised that diversity and composition of the rove beetles in the mature forest would be different from those in the plantations. We expected that reforestation with native species would have less harmful effects on rove beetles than reforestation with non-native species. In accordance with our hypotheses the overall number of rove beetle individuals and species, as well as the diversity of hygrophilous and decaying material dependent rove beetles were significantly lower in the plantations than in the mature oak forest. However, the overall species richness and the diversity of hygrophilous and decaying material dependent rove beetles were significantly higher in the native plantation compared to the non-native ones. There was no significant correlation between the diversity of these rove beetles and the soil moisture and decaying woody materials as limiting resources; thus, our study did not support the resource quantity hypothesis. The cover of herbs and shrubs, the soil temperature and soil pH were the most important factors controlling the diversity of rove beetles. Our results suggest that reforestation with native tree species provides more suitable habitat for rove beetles than non-native ones. However, it seems that rove beetle assemblages did not recover even after 40 years of reforestation with native tree species due to their specific ecological demands.

Keywords Diversity · Hygrophilous species · Mature oak forest · Native plantation · Non-native plantations · Resource quantity hypothesis

Introduction

Every year the area of planted forests increases by about 5 million hectares globally. In Europe plantation forest cover has reached 59 million hectares of which the percentage of non-native tree species was more than 12 % in 2010 (FAO 2010). The reason for this was that a substantial proportion of native forests was lumbered and replaced by monocultures of non-native tree species in the past (Magura et al. 2003; Thompson et al. 2003). In the second half of the twentieth century there were efforts to compensate for past deforestation and achieve timber self-sufficiency. It became a primary purpose to support a greater number of trees planted than cut in EU countries (Gold 2003). Several non-native tree species are stress-tolerant, fast growing, and have higher quality of wood compared to native deciduous tree species; therefore, these have been widely used throughout Europe during reforestation and afforestation (Baini et al. 2012). This kind of forest management was also widespread in Hungary. Thus, nearly half of the forested area were comprised of non-native species in the 1990s (ÁESZ 2008). Although the area of non-native plantations has decreased in the past few years, it still remains about 37 % of Hungarian forested areas (Wisnovszky 2014). The large amount of non-native plantation has altered the structure of forested areas, which has resulted in changes in the composition of the original flora

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✉ Dávid D. Nagy
david.nagy111@gmail.com

[1] MTA-DE Biodiversity and Ecosystem Services Research Group, Egyetem tér 1, Debrecen 4032, Hungary

[2] Department of Ecology, University of Debrecen, P.O. Box 71, Debrecen 4010, Hungary

and fauna (Magura et al. 2002; Roberge and Stenbacka 2014). Fortunately, in the last two decades serious efforts have been made to reforest with native species (Magura et al. 2015).

Several studies revealed that reforestation has significant effects on ground-dwelling arthropods (Finch 2005; Magura et al. 1997; Niemelä et al. 1993). In particular the direct destruction of original habitats by intensive pre- and post-treatments (clear-cutting, grubbing, tilling and deep loosening) causes significant changes in the structure of arthropod assemblages (Magura et al. 2002, 2015). The majority of published studies investigated the effects of reforestation and accompanying forest managements on ground beetles or spiders (Pohl et al. 2007). These taxa are mostly generalist predators and probably less sensitive to microclimate and food resources than saprophilous beetles, bryophytes, lichens and fungi (Paillet et al. 2010). Species requiring specific microclimate and food resources respond sensitively to the reduction of habitat diversity and microhabitat availability (Hjältén et al. 2007; Johansson et al. 2007; Paillet et al. 2010). Therefore, it is also necessary to investigate those taxa which are sensitive to changes in food resource quality and quantity (Niemelä et al. 2007). During the timber-oriented forest management several food resources and microhabitats, such as dead woods, humus, cavities, nests and fungi have been negatively impacted; these are indispensable for the specialist species (Bengtsson et al. 2000; Langor et al. 2008; Paillet et al. 2010).

Rove beetles (*Coleoptera: Staphylinidae*) are one of the largest families of beetles with more than 46,200 known species in the world (Newton et al. 2001). Most of them are predators of other arthropods, but several species are specialised in the utilisation of other food resources, for example decaying material, pollen, fungi and algae; in addition, some species are ectoparasitoids of other taxa (Pohl et al. 2008). The varied nutrition of rove beetles has important ecological roles in nutrient cycling and ecosystem productivity (Seevers and Herman 1978), which may affect ecosystem services. About half of the known species live in forest litter and they form one of the most common and ecologically important insect components of soil fauna. They are diverse and abundant, being mobile and relatively short-lived and species are taxonomically and ecologically well-known (Boháč 1999). They respond sensitively to abiotic and biotic changes and human disturbances (Magura et al. 2013).

With the increase of plantation forest and associated environmental changes, it is becoming more important to get detailed knowledge about the effects of non-native plantations on assemblages (Vilà et al. 2011). This motivated our research in which we studied the rove beetle assemblages of monospecific plantations of non-native tree species (black locust *Robinia pseudoacacia* L., Scots pine *Pinus sylvestris* L., red oak *Quercus rubra* L.), native oak (*Quercus robur* L.) plantation and mature oak forest as control.

In this study, we tested the following hypotheses: (1) diversity and composition of the rove beetles in the mature forest are different from those in the plantations due to the mechanical soil preparation before reforestation, and the light tilling until canopy closure of plantations. Mature forests have distinctive environmental conditions and substrate materials providing favourable microclimate and food resources for several specialist species (Paillet et al. 2010). These features are drastically altered by intensive forest management, causing a shift in the diversity and composition of rove beetles (Pohl et al. 2007). However, with ageing of native tree plantations the environmental conditions, such as accumulation of native leaf litter and decaying woody materials with associated organisms, become more similar to those of the mature forest. This increasing similarity in environmental conditions contributes to the recolonisation and establishment of permanent populations of ground-dwelling beetles (Brockerhoff et al. 2008; Magura et al. 2015). Therefore, we expected that the (2) reforestation with native tree species has less harmful effects on rove beetles than reforestation with non-native tree species. Our hypotheses are in accordance with the resource quantity hypothesis, assuming that the average supply rate of the limiting resources (such as soil moisture and decaying food resource) maintains a higher number of rove beetle individuals and species requiring humid microclimate and/or decaying food resources (hygrophilous and decaying material dependent species) in the control mature oak forest than in the plantations (Bartels and Chen 2010; Hart and Chen 2008; Stevens and Carson 2002). Moreover, we measured habitat characteristics, soil temperature, moisture and pH to determine whether they were predictors for diversity of rove beetles.

Materials and methods

Study area

The study area was located in the northern part of Debrecen city (Eastern Hungary), in a large, continuous forested region, in the Nagyerdő Forest Reserve Area (47°32′N; 21°38′E). Here, the typical native association is lowland oak forest (*Convallario-Quercetum roboris*) (Török and Tóthmérész 2004). Four monospecific plantation types and a mature oak forest were selected to investigate the impacts of reforestation on the rove beetle assemblages: (1) 135-year-old native mature lowland oak forest without management; it was used as control. English oak was the most numerous tree species in the closed tree canopy layer; common hawthorn (*Crataegus monogyna* Jacq.), elderberry (*Sambucus nigra* L.), field maple (*Acer campestre* L.) and black cherry (*Prunus serotina* Ehrh.) were most frequent in the shrub layer. The cover of herbs was moderate; the fallen, decaying woody materials were numerous. (2) 40-year-old native oak plantation (*Q. robur*); it was established after clear-cutting of mature native lowland oak forest stands by planting acorns. The shrub layer consisted of scattered individuals of *P. serotina*, while in the herbaceous layer *Alliaria petiolata* M.Bieb., *Urtica dioica* L., *Impatiens parviflora* DC., *Dactylis polygama* Horv., *Geum urbanum* L. were numerous. (3) In the 30-year-old black locust plantation boxelder and black cherry were most frequent in the shrub layer; the herb layer was dense (*Chelidonium majus* L., *Bromus sterilis* L., *Elymus caninum* L.). (4) In the 39-year-old Scots pine plantation there was a dense shrub layer; in the undergrowth vegetation American pokeweed (*Phytolacca americana* L.) was present with a high cover. (5) In the 31-year-old red oak plantation the shrub and the herb layers were missing. Black locust, Scots pine and red oak were the most common non-native tree species used in the reforestation of the north-eastern part of the Great Hungarian Plain. All the studied plantation types were established after clear-cutting of mature lowland oak forest stands. These were similarly cultivated by mechanical soil preparation before reforestation and light tilling during the management of the plantation to prevent weed establishment until canopy closure, which occurred after 15–20 years of reforestation. Plantations of age 30–40 years are usually regarded as being in the same age class, because the canopy is totally closed by that time and of a similar stand structure. Fallen and decaying wood was removed from the native and non-native plantations during management. For spatial replication two separated stands of all habitat types were investigated. All sampled stands were >3 ha. The distance between the studied stands was >300 m and all stands were separated by features such as footpaths, dirt roads and other forest stands from each other; therefore, the studied rove beetle assemblages in the stands could be considered as spatially independent replicates. All studied plantation stands were adjacent to mature oak forest stands. The soil type in the studied stands was identical, sandy soil with humus and there was no difference in the topography (elevation and slope) and drainage.

Sampling design

Rove beetles were collected at each stand using litter sifting. It is an efficient method to collect arthropods which are active in litter and debris (Martin 1977). Sampling points were selected using a metal frame (25 × 25 cm). Litter, soil and debris were removed from the 5 cm depth frame and sifted vigorously on a screen wire-mesh bottom (30 cm in diameter) with 1 cm in diameter size meshes, which was sewn to a cloth sleeve. Sifted litter samples were stored in sealed bags (Anderson and Ashe 2000). Rove beetles were extracted manually from each sample in the laboratory, and the specimens were preserved in 70 % alcohol (Shavrin 2009). All rove beetles taken in litter sifter samples were identified to species level using standard keys (Assing and Schülke 2011; Lohse 1974). Rove beetle species were classified according to their ecological demands based on Koch (1989) and Stan (2008). Saprophilous, coprophilous and xylodetriticol species were classified as decaying material dependent species.

Five randomly selected litter sampling plots (5 × 5 m) were assigned at each stand. Overall there were 50 samples (5 habitat types × 2 replicates × 5 samples). Samples were collected every third week from April to October in 2011. Litter sifter samples were taken randomly in the sampling plots at the first sampling date. At the further sampling dates the litter sifter samples were taken also randomly, at least 1 m from the earlier samples. Pitfall samples more than 10 m from each other are statistically independent for ground-dwelling beetles (Digweed et al. 1995). To provide statistically independent samples the litter sifter samples were at least 15 m apart from each other at each sample date. Each litter sampling plot was at least 25 m from the forest edge, in order to avoid any edge effect (Tóthmérész et al. 2014). For the statistical analyses, we pooled samples for the whole year.

We measured eight environmental variables that can affect the diversity of rove beetles (Irmler and Gürlich 2007; Magura et al. 2002). The soil temperature at 2 cm depth was measured next to every litter sample on the sampling days (Voltcraft DT-8820). We also estimated the percentage cover of leaf litter, decaying woody materials, herbs, shrubs and tree canopy within a circle of 1 m diameter around the litter sifter samples every sampling time. Furthermore, we collected soil samples next to every litter sample and we measured the moisture content and the pH value of soil in the laboratory using an electrochemical method (Thomas 1996). For the statistical analyses we used the average of measurements over the season.

Data analysis

Generalized Linear Models (GLMs) with a factorial design were used to test differences in the number of rove beetle individuals and species between the five habitat types. The habitat type and the spatial replicate were used as fixed factors. The response variables (number of individuals and species richness) were regarded as following a Poisson distribution accounting for overdispersion using the

Pearson Chi^2 (with log link function; Zuur et al. 2009). When the overall GLMs revealed a significant difference between the means, a LSD (least significant difference) test was performed for multiple comparisons among means.

GLMs were also used to analyse the relationship between the eight environmental variables and the number of rove beetle individuals and species, using a multiple regression design and forward stepwise model building (Wakefield 2013). We first fitted the full model containing all environmental variables. We evaluated models based on Akaike's Information Criterion (Fang 2011), and accepted the model with the lowest AIC as the final model. In the final model the dependent variables (species richness and abundance) were regarded as following a Poisson distribution (with log link function, accounting for overdispersion). GLM analyses were performed using STATISTICA 8.0 (StatSoft Inc. 2010).

Dissimilarity of the species composition of litter sifter samples was calculated by the Bray-Curtis index of dissimilarity based on the abundances, and it was displayed by non-metric multidimensional scaling (NMDS) (Borcard et al. 2011). For this analysis we used the NuCoSA 1.05 package (Tóthmérész 1993).

Results

Altogether 1,542 individuals belonging to 92 species were collected by litter sifter. In the mature oak forest 60 species and 476 individuals were caught, while in the native oak plantation 44 species and 338 individuals were caught. Thirty-seven species and 265 individuals were captured in the black locust plantation; 33 species and 252 individuals were collected from the Scots pine plantation and 211 individuals belonging to 47 species were sampled in the red oak plantation ("Appendix"). The most numerous species was *Gabrius osseticus* (Kol., 1846), which made up 8.2 % of the total catch. This species was also the most numerous in the native oak plantation. *Sepedophilus pedicularius* (Grav., 1802) was dominant in the black locust plantation, while in the Scots pine plantation *Pselaphus heisei* Herbst, 1792 was the most frequent. In the red oak plantation *Omalium caesum* Grav., 1806 was the most abundant. In the mature oak forest *Geostiba circellaris* (Grav., 1806) was the most numerous species.

We found that the spatial replicate was a significant factor only for the overall number of individuals ("Appendix"). Significant differences were observed in the overall number of rove beetle individuals and species among the studied habitats. Significantly fewer individuals and species were sampled in the plantations than in the mature oak forest (for the number of individuals: Wald statistic = 51.36; $df = 4{,}4$; $p < 0.0001$; for the number of species: Wald statistic = 87.62; $df = 4{,}4$; $p < 0.0001$, respectively, Fig. 1a, b). The overall number of rove beetle species was significantly higher in the native plantation than in the non-native ones, while the overall number of individuals was significantly higher in the native plantation than in the Scots pine and red oak plantations (Fig. 1a, b). There was no significant difference in the overall number of individuals between the native and black locust plantations (Fig. 1a).

Both the number of hygrophilous rove beetle individuals and species were significantly greater in the mature oak forest than in the plantations. Moreover, these variables were significantly greater in the native plantation compared to the non-native ones (for the number of individuals: Wald statistic = 66.32; $df = 4{,}4$; $p < 0.0001$, and for the number of species: Wald statistic = 59.66; $df = 4{,}4$; $p < 0.0001$, respectively, Fig. 2a, b). There were no significant differences in these variables among the non-native plantations (Fig. 2a, b). Similarly, the number of decaying material dependent species and their abundance were significantly greater in the mature oak forest than in the plantations (for the number of individuals: Wald statistic = 50.04; $df = 4{,}4$; $p < 0.0001$, and for the number of species: Wald statistic = 75.48; $df = 4{,}4$; $p < 0.0001$, respectively, Fig. 2c, d). Furthermore, these variables were significantly greater in the native plantation than in the non-native ones (Fig. 2c, d).

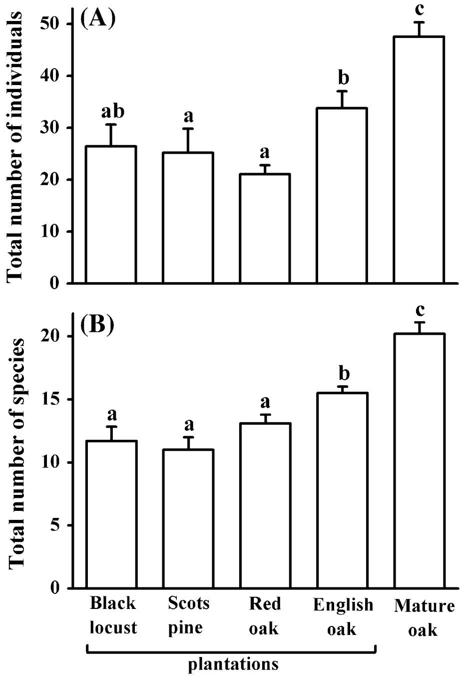

Fig. 1 Number of rove beetle individuals (**a**) and species (**b**) per sampling point (±SE) in the studied habitat types. Means with different *letters* indicate a significant ($p < 0.05$) difference by LSD test

The cover of canopy, shrubs, herbs, litter and decaying woody materials and the soil properties (soil temperature, soil moisture and pH) differed between the habitat types (Table 1). The red oak plantation had the most closed canopy; the herb and shrub layers were thin. In the black locust plantation the soil temperature was higher than in the other habitats. The mature oak forest was characterised by the highest cover of decaying woody materials. The soil moisture and the pH value were the highest in the mature oak forest (Table 1).

Generalized linear models (GLMs) showed that the soil pH, the soil temperature and the cover of shrubs and herbs were the most important factors correlated with the diversity of rove beetles in the studied habitats (Table 2). The cover of shrubs was a positive predictor for the abundance and species richness of hygrophilous rove beetles, whereas the cover of herbs also showed a positive correlation with the overall number of individuals, the number of hygrophilous individuals and species, and the number of decaying material dependent individuals. Our results showed a significant negative correlation between the soil temperature and the total number of individuals and species, the number of hygrophilous individuals and species, and the number of decaying material dependent individuals and species. The total number of species, the number of hygrophilous species, and the number of decaying material dependent individuals and species increased as the soil pH increased (Table 2).

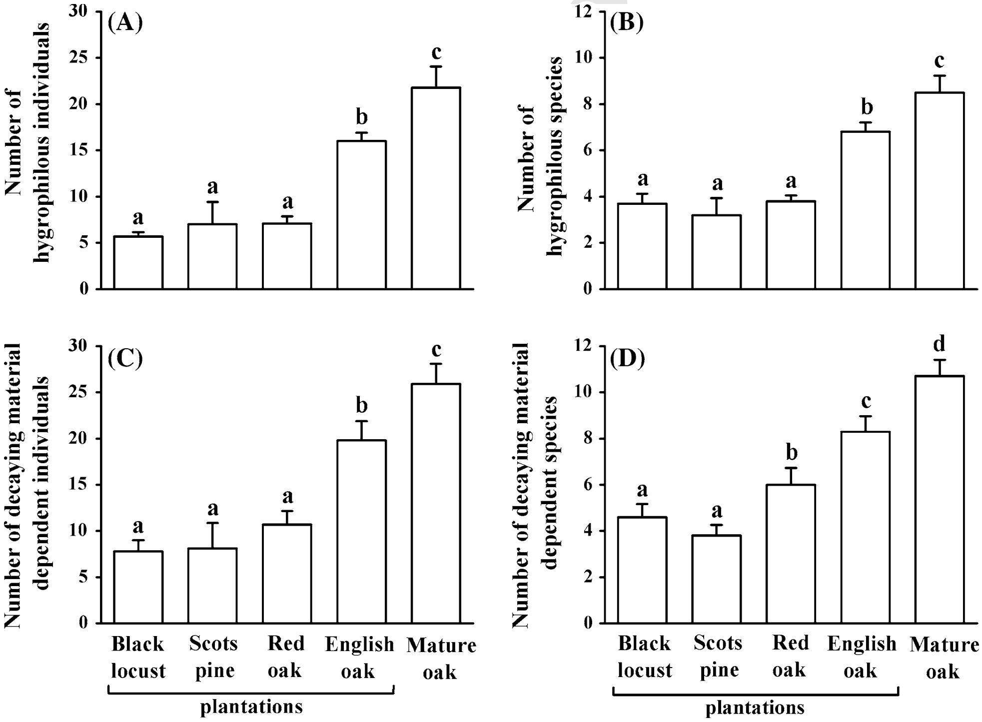

Fig. 2 Number of the hygrophilous rove beetle individuals (**a**) and species (**b**), and decaying material dependent rove beetle individuals (**c**) and species (**d**) (±SE) in the studied habitat types. Means with different *letters* indicate a significant ($p < 0.05$) difference by LSD test

Table 1 Average values (±SE) of the studied environmental variables

Environmental variables	Black locust plantation	Scots pine plantation	Red oak plantation	Native oak plantation	Mature oak forest
Canopy cover (%)	55.3 ± 2.9	49.2 ± 3.1	83.8 ± 1.2	70.0 ± 4.7	62.9 ± 7.3
Cover of shrubs (%)	34.3 ± 7.7	36.5 ± 5.6	14.1 ± 4.3	32.2 ± 8.0	50.7 ± 6.0
Cover of herbs (%)	23.3 ± 4.5	15.9 ± 2.1	7.3 ± 2.8	12.6 ± 2.1	12.2 ± 3.3
Cover of leaf litter (%)	87.8 ± 3.2	86.0 ± 5.0	93.1 ± 4.4	92.6 ± 2.7	78.0 ± 5.9
Cover of decaying woody materials (%)	7.2 ± 1.7	10.7 ± 1.2	9.0 ± 1.2	7.7 ± 0.9	14.1 ± 1.6
Soil moisture (%)	6.6 ± 0.6	10.2 ± 1.2	4.0 ± 0.2	7.6 ± 0.5	13.4 ± 0.8
Soil temperature (°C)	17.5 ± 0.1	16.4 ± 0.1	16.1 ± 0.2	16.3 ± 0.1	15.8 ± 0.1
Soil pH	5.1 ± 0.1	4.4 ± 0.0	5.0 ± 0.1	5.0 ± 0.1	5.6 ± 0.2

Table 2 Relationship between the number of rove beetle individuals, species and the studied variables by generalized linear models (GLMs) using the multiple regression design and the forward stepwise model building

	Total no. of individuals	Total no. of species	No. of hygrophilous individuals	No. of hygrophilous species	No. of decaying material dependent individuals	No. of decaying material dependent species
Test of the model						
r	0.6379	0.6847	0.6541	0.6500	0.6392	0.6619
F	4.9166	13.534	6.5815	8.2312	6.0808	11.957
p	***	***	***	***	***	***
df	6, 43	3, 46	5, 44	4, 45	5, 44	3, 46
Canopy cover (%)	Not entered	Not entered	Not entered	Not entered	Not entered	Not entered
Cover of shrubs (%)	ns	Not entered	+*	+*	ns	ns
Cover of herbs (%)	+*	ns	+*	+*	+*	Not entered
Cover of leaf litter (%)	Not entered	Not entered	Not entered	Not entered	Not entered	Not entered
Cover of decaying woody materials (%)	ns	Not entered	ns	Not entered	ns	Not entered
Soil moisture (%)	ns	Not entered	Not entered	Not entered	Not entered	Not entered
Soil temperature (°C)	−**	−***	−***	−***	−***	−***
Soil pH	ns	+***	ns	+*	+*	+***

Significant negative (−) and significant positive (+) relationships are marked

ns not significant, *not entered* the variable was not entered into the model

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

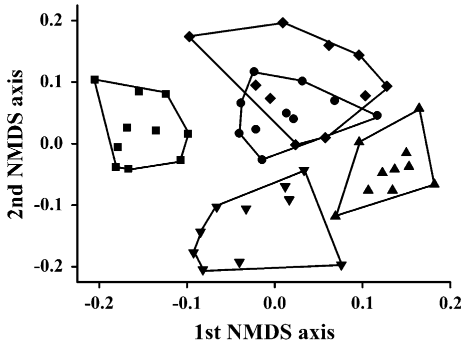

Fig. 3 Multidimensional scaling of the rove beetle assemblages based on the abundances using the Bray-Curtis index of dissimilarity. Notations: *black up-pointing triangle*—*black* locust plantation, *black down-pointing triangle*—Scots pine plantation, *black diamond suit*—*red* oak plantation, *black circle*—native oak plantation, *black square*—mature oak forest

The rove beetle assemblages of the mature oak forest were separated from the assemblages of the samples from the plantations along the first axis of the NMDS. The rove beetle assemblages of the samples from the native oak plantation and red oak plantation were similar to each other (stress value: 0.2516; Fig. 3).

Discussion

Our study showed that the establishment of plantations after clear-cutting of native, mature oak forest stands caused changes in the diversity and composition of rove beetles. The overall number of rove beetle individuals and species were significantly lower in the plantations compared to the mature oak forest. Similarly to our results, several previous studies demonstrated that establishment of plantations do not provide suitable habitat for invertebrates and causes changes in ground-dwelling beetle assemblages (Magura et al. 2003; Paritsis and Aizen 2008; Roberge and Stenbacka 2014). Intensive forest treatments like the clear-cutting of mature forest stands, the mechanical soil preparation before reforestation and the cultivation by light tilling during the management drastically alter the original habitats (Magura et al. 2015). These treatments eliminate the specific microsites and considerably alter the habitat structure and microclimatic conditions, causing shift in the ground-dwelling beetle assemblages (Magura et al. 2006; Roberge and Stenbacka 2014). In the case of ground beetles almost all studies confirmed that clear-cutting of native forests and the subsequent treatments caused considerable changes in the composition of assemblages, which were most markedly detectable in the early phase (1–3 years) of reforestation (Magura et al. 2003, 2015; Niemelä et al. 2007).

In the studied area, trees were planted in parallel rows in the plantations and spaces between the rows were regularly managed until the closure of the canopy, which created an open, bare soil surface and allowed sunlight to penetrate more deeply, influencing the soil temperature and soil moisture (Anderson et al. 1976). The depth of tilth, the humus content and physical properties of the soil are also important determinants of the soil temperature and soil moisture in plantations (Anderson et al. 1976; Keenan and Kimmins 1993). Our results showed that the soil moisture was lower, while soil temperature was higher in the plantations compared to the mature oak forest, resulting in a lower diversity of hygrophilous rove beetle species in the plantations. The results of multiple regression analysis showed a negative correlation between soil temperature and the diversity of rove beetles. Szujecki (1966) and Irmler (1993) also pointed out that soil moisture was an important predictor to the diversity of rove beetles. Clear-cutting causes rapid degradation of humus that accumulated over several decades. A substantial part of the residuary humus layer is eliminated during the management of trunk tracts. These changes lead to soil acidification and decreasing storage capacity for water in the plantations (Johnson 1992). In our study the soil pH was lower in the plantations than in the oak forest and there was a positive correlation between the soil pH and the species richness of rove beetles. Buse and Good (1993) and Irmler and Gürlich (2007) also underlined the importance of soil pH controlling the rove beetles' diversity. After the reforestation, regular cultivation by light tilling influences the structure of the leaf litter, and the development of the humus layer; these changes further constrain the diversity of rove beetles (Andersson et al. 2004; Keenan and Kimmins 1993). We found no significant correlation between the cover of litter, the tree canopy cover and the diversity of rove beetles, while Rose (2001) suggested that leaf litter and tree canopy cover could be important factors determining the diversity of rove beetles. In our investigation the cover of herbs was an important predictor controlling the diversity of rove beetles, and the cover of shrubs showed a positive correlation with the diversity of hygrophilous species and individuals. During the establishment of plantations the decaying woody materials are eliminated; thus, that which is present is younger (fresher) and the amount is smaller in the plantations than in the mature forests (Spies and Cline 1989). The amount of decaying woody material may influence the diversity of the decaying material dependent species. Hammond et al. (2004) showed that the richness of specialist species (predators, fungivorous and scavengers) increases from habitat with fresh woody materials to habitat with highly decaying woody materials. The increasing microhabitat diversity within decaying woody materials provides suitable conditions for specialist rove beetle species (Siitonen 2001). Roberge and Stenbacka (2014) also showed that the abundance of wood- and cambium specialist beetles (including several rove beetle species) and the species richness of these beetles were significantly lower in introduced non-native lodgepole pine stands than in the native Scots pine ones. Our results showed that the cover of decaying woody materials was the highest in the mature oak forest, but it did not show a significant correlation with the diversity of rove beetles.

Several previous studies showed that the quantity, size and age of the decaying substrates could be other important factors on the spatial pattern of specialist species (Hammond et al. 2004; Hanski and Cambefort 1991). Dead wood, humus, carrions, nests, feces and other resources are indispensable for specialist rove beetle species (Boháč 1999; Magura et al. 2013). Establishment of monospecific plantations causes nutrient losses and leads to declines in soil fertility and leaf litter production, and it alters the microbial community that is known to be a major contributor of enzyme activities and decomposition processes (Fang et al. 2013; Saswati and Vadakepuram 2010). Thus, habitat alterations can reduce and slow down the nutrient cycling and decomposition processes in the plantations contributing to the reduction of the diversity of specialist rove beetles. Our results did not support the resource quantity hypothesis, because there was no significant correlation between the species richness and the number of individuals of hygrophilous and decaying material dependent rove beetles and the studied limiting resources. The possible reason is that the quality of decaying woody materials and soil parameters could be more important drivers in the diversity of hygrophilous and decaying material dependent rove beetles than the quantity of these limiting resources.

The non-native plantations are more harmful for the original ground-dwelling beetle assemblages compared to the native plantations, since the environmental conditions change more in the non-native plantations than in the native plantations (Robson et al. 2009). Our results showed that the overall number of rove beetle species was significantly lower in the non-native plantations than in the native oak plantation. The reforestation with non-native tree species eliminates the original microsites (such as native leaf litter layer and woody debris) and permanently alters the microclimatic conditions, vegetation structural complexity and development of litter and humus layers, which promote the disappearance of the sensitive specialist species (Brockerhoff et al. 2008; Magura et al. 2003). Moreover, these alterations in non-native plantations hamper the regeneration of the favourable environmental conditions. Thus, non-native plantations do not provide suitable conditions for recolonisation of rove beetle species with specific microclimate and food resource demands even after 20 years of canopy closure.

The closed native oak plantation is similar in environmental conditions (native leaf litter, herbaceous and humus layer, native decaying woody materials) to the mature oak forest; therefore, the native plant and insect species may recover easily. Moreover, the nearby mature forest stands provide a local source of native dispersal agents, which result in rapid vegetation and microclimate regeneration within the native oak plantation (Brockerhoff et al. 2008). Thus, reforestation with native tree species facilitates the forest regeneration and accordingly to the recolonisation of ground-dwelling beetles after some 10 years of reforestation (Buddle et al. 2006; Magura et al. 2015; Taboada et al. 2008). The accumulation of native leaf litter and decaying woody materials with associated organisms such as herbs, fungi, bacterium and insects create suitable microclimate and food resources for the specialist species, contributing to the recovery of rove beetles. Although the cover of decaying woody materials was similar in the plantations, the number of hygrophilous and decaying material dependent species and their abundance were significantly higher in the native oak plantation compared to the non-native ones. Native plant debris may be easier and more effectively processed by the native decomposer microbes; thus, decaying food resources with higher quality result in a higher number of specialist species in the native plantation (Rudgers and Orr 2009). Despite the fact that the number of rove beetle individuals and species were higher in the native oak plantation compared to the non-native ones, there were still significantly more in the mature oak forest. Summarising, our results did not suggest that rove beetle assemblages can totally recover in native oak plantations after 40 years of reforestation.

Management implications and further perspectives

Our results demonstrated that clear-cutting of mature oak forest stands, creating of plantations and the post-treatments of the plantations (removal of litter, herbs, shrubs and fallen woods) had detrimental effects on the rove beetle assemblages. These habitat alterations change the original vegetation structure and microclimate; furthermore they reduce and slow down nutrient cycling and decomposition processes (Barlow et al. 2007; Jha et al. 1992; Roberge and Stenbacka 2014). These changes significantly influenced the hygrophilous and decaying material dependent rove beetles. However, it seems that these species recover easier in the native oak plantation than in the non-native ones.

Based on our results, the establishment of additional non-native plantations is not advised, because local rove beetle diversity and environmental services could be better enhanced in native oak plantations than in non-native ones. Our findings suggest that recovery of rove beetle assemblages is likely to take more than 40 years even in native oak plantations. We recommend that the mechanical soil preparation before reforestation and the cultivation by light tilling should be omitted during forest management and it is necessary to use new and more efficient forestry practices maintaining or even enhancing biodiversity (Magura et al. 2006). For example, the seed tree method can provide seeds for natural regeneration, the shelterwood harvesting method produces shady conditions for seedlings, furthermore group selection and single tree selection create multi-aged stands, maintaining mature or late-successional forest characteristics and species assemblages (Magura et al. 2015).

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Appendix

See Tables 3 and 4.

Table 3 Ecological demands and the number of individuals of sampled rove beetle species

Species	Ecological demands	BL	SP	RO	NO	M
Alaobia scapularis		2	0	0	0	0
Aleochara bipustulata	d	0	0	0	1	0
Aleochara lanuginosa	d	1	0	0	0	0
*Amauronyx maerkelii**		0	0	0	0	1
Anthobium atrocephalum	d	0	3	0	4	6
Atheta benickiella		0	0	0	0	1
Atheta gagatina	d	0	2	6	2	2
Atheta ganglbaueri		0	0	1	0	0
Atheta harwoodi	d	0	0	0	0	1

Table 3 continued

Species	Ecological demands	BL	SP	RO	NO	M
Atheta sodalis		0	0	1	0	0
Atheta voeslauensis		0	0	5	1	0
*Batrisodes adnexus**		0	0	0	0	1
Bolitobius castaneus		1	0	0	1	1
Bolitochara bella	d	0	0	2	1	1
Brachida exigua		0	0	2	0	3
*Bryaxis sp 1.**		0	17	0	0	17
*Bryaxis sp 2.**		2	2	2	0	15
*Bryaxis carinula**		2	8	3	15	18
*Bryaxis curtisii orientalis**		0	9	1	7	13
Dropephylla ioptera	d	0	0	0	0	12
Falagrioma thoracica		0	0	0	0	1
Gabrius osseticus	h, d	19	13	19	44	32
Geostiba circellaris	h, d	0	20	0	4	50
Gyrohypnus angustatus	h	1	1	0	0	2
Gyrophaena fasciata		0	0	0	1	0
Gyrophaena joyi		0	0	1	0	0
Gyrophaena joyioides		0	0	0	0	3
Habrocerus capillaricornis	d	0	0	4	1	12
Heterothops dissimilis	d	11	2	5	19	2
Ischnosoma splendidum	h, d	0	4	0	1	0
Lathrobium geminum	h, d	0	0	0	4	0
Liogluta granigera		0	0	0	0	14
Liogluta longiuscula	h	0	0	0	0	3
Medon fusculus		0	0	0	3	21
Metopsia similis	d	24	28	12	23	15
Mocyta fungi	h, d	1	2	3	20	6
Mocyta negligens		0	0	0	0	1
Mocyta orbata	h, d	3	0	0	3	8
Mycetoporus erichsonanus		0	0	1	0	1
Mycetoporus eppelsheimianus		0	1	2	5	1
Mycetoporus forticornis		0	0	1	0	0
Mycetota laticollis	d	0	0	0	1	0
Ocalea badia	h	0	0	1	1	6
Ocypus mus		0	0	1	0	0
Ocypus nitens	h	3	0	0	0	1
Omalium caesum	h, d	1	1	24	22	35
Omalium oxyacanthae	d	0	0	1	0	0
Omalium rivulare	h, d	0	0	2	0	8
Ontholestes haroldi	d	4	1	3	2	0
Othius punctulatus		0	1	6	2	1
Oxypoda abdominalis		6	0	7	7	1
Oxypoda acuminata	h, d	1	0	4	3	5
Oxypoda flavicornis	h	0	1	1	0	3
Oxypoda opaca	d	0	0	1	1	0
Oxypoda praecox	h	0	9	0	0	0
Pella laticollis		0	0	0	0	33
Pella ruficollis		0	0	0	0	8

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Table 3 continued

Species	Ecological demands	BL	SP	RO	NO	M
Philonthus cognatus	d	1	0	0	0	0
Phyllodrepa melanocephala	d	0	0	0	0	4
Pselaphus heisei		9	54	8	6	26
Quedius curtipennis	h, d	0	0	0	0	1
Quedius fuliginosus	h	0	0	0	0	1
Quedius limbatus	h, d	1	3	6	17	33
Quedius scintillans	d	0	0	1	0	2
Rugilus rufipes	h, d	1	0	3	9	9
Rugilus subtilis	d	2	0	1	1	0
Sepedophilus marshami		5	10	19	28	5
Sepedophilus immaculatus	d	0	0	2	0	0
*Sepedophilus obtusus**		10	3	15	17	0
Sepedophilus pedicularius		44	1	2	0	0
Sepedophilus testaceus		0	0	4	1	1
Scaphium immaculatum		3	2	2	1	0
Scaphidium quadrimaculatum		0	0	1	0	1
Stenus ater	h	1	0	0	0	0
Stenus clavicornis		1	0	0	0	0
Stenus humilis	h	17	8	3	11	0
Stenus ludyi	h	3	7	0	7	1
Stenus ochropus		31	19	3	4	1
Sunius fallax		41	9	11	21	6
Tachinus fimetarius	d	0	0	1	0	1
Tachyporus atriceps		0	8	0	0	2
Tachyporus chrysomelinus	d	0	0	0	1	0
Tachyporus hypnorum	h, d	4	1	5	13	13
Tachyporus nitidulus	d	1	1	2	1	1
Tasgius morsitans		0	0	0	0	1
Thinonoma atra	h	0	0	0	0	1
Xantholinus dvoraki		4	0	0	0	0
Xantholinus linearis	d	2	0	0	0	0
Xantholinus longiventris	h, d	1	0	0	0	0
Xantholinus tricolor		1	1	0	0	0
Zyras collaris	h	0	0	0	1	0
Zyras haworthi		0	0	0	0	1
Total number of species		37	33	47	44	60
Total number of individuals		265	252	211	338	476

BL—black locust plantation, SP—Scots pine plantation, RO—red oak plantation, NO—native oak plantation, M—mature oak forest, h—hygrophilous species; d—decaying material dependent species (*there is no available information)

Table 4 Factorial GLMs showing differences in total number of individuals and species, number of hygrophilous individuals and species, number of decaying material dependent individual and species between studied habitat types and spatial replicates

Variable	Source	*df*	Wald	*p*
Total number of individuals	Intercept	1	5456.07	***
	Habitat type	4	51.36	***
	Spatial replicate	1	4.01	*
Total number of species	Intercept	1	10593.50	***
	Habitat type	4	87.62	***
	Spatial replicate	1	0.00	ns
Number of hygrophilous individuals	Intercept	1	985.04	***
	Habitat type	4	66.32	***
	Spatial replicate	1	0.00	ns
Number of hygrophilous species	Intercept	1	821.74	***
	Habitat type	4	59.66	***
	Spatial replicate	1	0.06	ns
Number of decaying material dependent individuals	Intercept	1	1131.22	***
	Habitat type	4	50.04	***
	Spatial replicate	1	0.00	ns
Number of decaying material dependent species	Intercept	1	1583.31	***
	Habitat type	4	75.48	***
	Spatial replicates	1	0.04	ns

ns not significant

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

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