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Recovery of surface-dwelling assemblages (Coleoptera: Carabidae, Staphylinidae) during clear-cut originated reforestation with native tree species

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Abstract

Background and purpose: *Timber-oriented forest management has an important impact on biodiversity in forest ecosystems. Recovery dynamics of two groups of beetles (Coleoptera: Carabidae, Staphylinidae) were studied after reforestation with native English oak (*Quercus robur*). We expected that reforestation with heavy site preparation causes a shift in the diversity of surface-dwelling beetles in early phases of reforestation. Moreover, we tested the habitat specialist hypothesis, assuming that diversity of forest specialist species will be lower in early phases with open canopy than later phases of reforestation after the canopy closure.*

Materials and methods: *We compared litter sifter samples among mature (130-year-old) oak forest, and recently established (5-year-old), young (15-year-old), middle-aged (45-year-old) reforestations.*

Results: *Our results showed that diversity of ground beetles was the highest in the recently established reforestation, while it was the lowest in the mature oak forest. Contrarily, diversity of rove beetles was the lowest in recently established reforestation and it was the highest in the mature oak forest. In agreement with the habitat specialist hypothesis, the diversity of forest specialists of both taxa was lower in the recently established reforestation than in the young and middle-aged reforestations as well as mature forest.*

Discussion: *Our results suggested that clear-cutting of mature forest, site preparation before reforestation and cultivation by light tilling in early phases of reforestation have detrimental effects on forest specialist rove beetles and ground beetles. However, reforestation with native species could be a feasible management method in pannonic mesophile sand steppe, because forest specialist species can recover after the canopy closure.*

INTRODUCTION

Timber-oriented forest management has a crucial impact on the structure and function of forest ecosystems. It also has a harmful effect on biodiversity, as several groups of animals, fungi, and plants are sensitive to anthropogenic disturbance and environmental changes *(1, 2)*. The cover of planted and naturally regenerated forests with human interventions accounted for 64 percent of the world's forest area in 2010, while cover of primary forests has been steadily decreasing since 2000 *(3)*. Recent European Union commitments have highlighted the need to halt biodiversity loss and promote sustainable management, and have included in the Natura 2000 network *(4)*. In spite of these measures the designated forest area for conservation of biodiversity was still 4.6 percent of European forests in 2015 *(5)*.

During forest management there are important decisions; selection of tree species (native, non-native species), sustainable practices, such as even-aged (modified clear-cutting, seed tree method and shelterwood harvesting) and uneven-aged (group selection, single tree selection) regeneration methods *(2, 6)*. Well-chosen forest practices contribute to maintaining forest biodiversity, because these practices have less intensive and less harmful impacts on environment than conventional clear-cutting model with soil preparation *(7)*. Nevertheless, the conventional clear-cutting of mature forest stands and soil preparation before reforestation are still widely used throughout Europe *(8)*. This forest practice is also commonly used by forestry in north-eastern part of the Great Hungarian Plain, Hungary *(2)*. Several previous studies revealed that clear-cutting of mature forest and reforestation with coniferous tree species alter the original landscape and cause changes in environmental conditions, resulting a shift in composition and diversity of surface-dwelling beetle assemblages *(9–11)*. However, only a few papers focus on recovery dynamics of surface-dwelling beetle assemblages in chronosequence of deciduous reforestation after clear-cutting *(2, 12)*.

Among surface-dwelling beetles, the ground beetles (Coleoptera: Carabidae) are the most frequently studied family with respect to the effects of forest management on invertebrates *(13)*. Ground beetles are good colonisers and generalist predators or polyphagous feeders, taxonomically and ecologically well-known and they are sensitive to environmental changes. Study of other taxa may also be expedient to get more details about the effects of forest management practices, because different taxa can respond differently to anthropogenic and natural disturbances *(13)*. Rove beetles (Coleoptera: Staphylinidae) are also a common beetle family of litter and soil fauna *(14)*. Similarly to ground beetles many species are good flier and predators of arthropods. However, some species are flightless and they utilize other food resources (decaying materials, pollen, fungi). They respond sensitively to habitat alteration and human disturbance, furthermore they have high species richness and abundance in worldwide (except open water surface and area above snowline), allowing their investigation as bioindicator *(14, 15)*.

In this paper we focused on the recovery dynamic of two surface-dwelling groups (ground beetles and rove beetles) in stages of a silvicultural cycle: 130-year-old mesophile sand steppe oak forest (*Convellario-Quercetum roboris*), and recently established, young and middle-aged reforested stands of English oak (*Quercus robur*). We expected that (i) heavy site preparation before reforestation (clear-cutting, grubbing, tilling) will cause a shift in diversity of surface-dwelling beetles in early phases of reforestation (1–5 years after the clear-cutting) *(2, 16)*. We also expected that disturbance generated by site preparation will reduce with ageing of reforested stands and the environmental conditions become more similar to the mature native forest after the canopy closure, contributing to the recovery of forest specialist surface-dwelling species *(2)*. Habitat specialist hypothesis is one of the most frequently used assumptions to test of human disturbances, supposing that characteristic specialist species of original habitat will decrease after human disturbance *(17)*. Therefore, we tested the (ii) habitat specialist hypothesis, assuming that diversity of forest specialist ground beetle and rove beetle assemblages will be lower in the recently established reforestation than in the young and middle-aged reforestations as well as in the mature forest.

MATERIAL AND METHODS

Study area

The study area was located in the North-Eastern part of the Great Hungarian Plain near to Debrecen city in Hungary (47°32'N; 21°38'E). Pannonic mesophile sand steppe oak forest is the typical native association in this region *(18)*. Chronosequence of a silvicultural cycle was selected to study the recovery dynamic of surface-dwelling beetles: (i) mature mesophile sand steppe oak forest (130-year-old) that had been selectively cut historically but never clear-felled; the English oak was the most numerous tree species in the closed tree canopy; shrub layer was moderate (*Crataegus monogyna*, *Sambucus nigra*, *Acer campestre* and *Prunus serotina*); in the herb layer among others *Polygonatum latifolium, Alliaria petiolata, Salvia glutinosa, Circaea lutetiana, Impatiens parviflora* and *Geum urbanum* were present. In the mature oak forest the fallen, decaying woody materials were abundant. The (ii) recently established English oak reforestation (5-year-old) with open, bare soil surface. It was cultivated by light tilling during forest management. *Quercus robur* and *Robinia pseudoacacia* were present in the shrub layer and the understory vegetation was dense (*Convallaria majalis, Polygonatum latifolium, Calamagrostis epigeios, Elymus caninus, Digitaria sanguinalis*). In the (iii) young English oak reforestation (15-year-old) with closed canopy cover, the shrub layer consisted of *Acer campestre* and *Prunus serotina*, while in the herb layer *Chelidonium majus, Bromus sterilis, Elymus caninus* were numerous. The (iv) middle-aged English oak reforestation (45-year-old); in the shrub layer individuals of *Prunus serotina* showed a scattered pattern, while in the herbaceous layer *Alliaria petiolata, Urtica dioica*, *Impatiens parviflora* and *Dactylis polygama* were most frequent.

All studied reforestations were established after clear-cutting of mature oak forest stands by planting native, English oak acorns. Fallen and decaying wood was removed from the reforestations during management. For spatial replication two separated stands (>3ha) of stages of the silvicultural cycle were investigated. Surface-dwelling beetle assemblages could be considered as spatially independent replicates due to distance (>300 m) and features (footpath, dirt roads and other forest stands) between the studied stands.

Sampling design

Both studied taxa were collected at each stand using litter sifting method. Previous studies showed that this method is efficient to collect arthropods which are active in soil, woody and litter debris *(19, 20)*. Five randomly selected litter sampling plots (5 × 5 m) were assigned at each replicates. In the sampling plots a metal frame (25 × 25 × 5 cm) was used to select the sampling quadrate, whereof soil, litter and woody debris were removed and those were sifted with a litter sifter *(6)*. Sampling quadrates were located randomly in sampling plots. These plots were at least 15–25 m apart from each other to provide statistically independent samples, and 30 m from the forest edge in order to avoid any edge effect (*6, 21, 22)*. Overall there were 40 litter samples (4 stages × 2 replicates × 5 litter samples). Litter samples were collected every third week from April to October in 2011. Collected beetles were extracted manually from each sample in the laboratory and preserved in 70% alcohol *(23)*.

Data analysis

All studied surface-dwelling beetles in litter sifter samples were identified to species level using standard keys *(24–26)*. For the statistical analyses, we pooled samples for the whole year.

Diversity profiles of the ground beetle and rove beetle assemblages were calculated using the Rényi diversity function by BiodiversityR program package *(27, 28)*.

The Rényi diversity, $HR(\alpha)$ is defined as:

$$HR(\alpha) = \frac{1}{1-\alpha}\left(\log \sum_{i=1}^{S} p_i^{\alpha}\right),$$

where p_i is the abundance of the *i*-th species, S the total number of species and α is the scale parameter ($\alpha \geq 0, \alpha \neq 1$).

At four values of the scale parameter α, the Rényi diversity index value relates to classical diversity indices *(29, 30)*: (i) at $\alpha = 0$, the value of the Rényi diversity is the logarithm of the number of species; (ii) at $\alpha \to 1$, the Rényi diversity is the same as the Shannon diversity; (iii) at $\alpha = 2$, the value of the Rényi diversity is related to the Simpson diversity, and (iv) at $\alpha \to +\infty$, the value of the Rényi diversity is closely related to the Berger-Parker dominance index *(31)*.

The Rényi diversity is sensitive to rare species at small values of the scale parameter; as the scale parameter increases, the diversity value is increasingly influenced by the common species. Near infinity, only the abundance of the most common species will determine the diversity. The assemblage whose diversity profile runs above the other ones (the diversity profiles do not intersect each other) is unequivocally more diverse than the other assemblages. By contrast, if the profiles cross each other, the assemblages cannot be unequivocally ordered, because one assemblage is more diverse for the rare species, while another is more diverse for the common ones *(17)*.

Due to different species pools and local conditions the diversity of the total assemblage may show idiosyncratic responses to different stages of silvicultural cycle; therefore, the assemblages of forest specialist species were also studied. Categorisation of a species as „forest specialist species" was based on the classification of Koch *(32)* and Hůrka *(26)* and also on our field experience (Appendix 1).

RESULTS

Altogether 1447 individuals of studied surface-dwelling beetles belonging to 135 species were trapped during the study; of which 314 individuals were ground beetles, belonging to 43 species and 1133 individuals were rove beetles, representing 92 species. Number of ground beetle species (26 including 2 forest specialist species) was the highest, while the number of rove beetle species (18 including 0 forest specialist species) was the lowest in the recently established reforestation; 7 forest specialist species from 17 ground beetle species and 8 forest specialist species from 46 rove beetle species were captured in the young reforestation; 17 ground beetle species (8 forest specialist species) and 45 rove beetle species (8 forest specialist species) were collected in the middle-aged reforestation; the lowest ground beetle species richness (12 species including 5 forest specialist species) and the highest rove beetle species richness (58 species including 11 forest specialist species) were observed in the mature forest (Appendix 1).

Differences were observed in the diversity of ground beetle and rove beetle assemblages among the studied stages of silvicultural cycle. Our results showed that the recently established reforestation supported the most diverse ground beetle assemblage, and the assemblage was the least diverse in the mature oak forest (Fig. 1A). Contrary to ground beetles, the diversity of rove beetle assemblages was the lowest in the recently established reforestation and the highest in the mature oak forest (Fig. 1B). Diversity profiles of both beetle assemblages in young and middle-aged reforestations are not comparable, since the diversity profiles are intersected to each other (Fig. 1A and B).

The diversity of forest specialist ground beetle assemblages was the lowest in the recently established reforestation (Fig. 2A). Middle-aged reforestation had more diverse forest specialist ground beetle assemblage over the entire range of the scale parameter than recently estab-

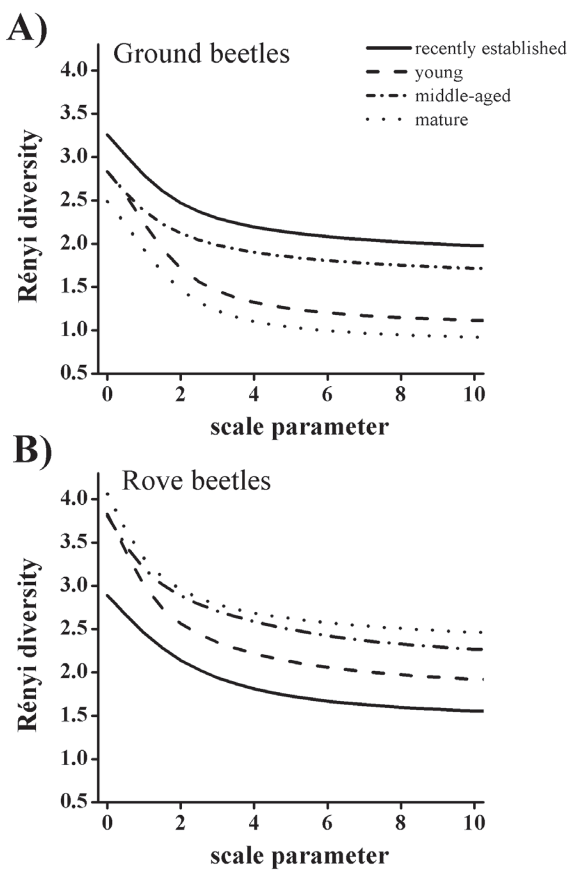

Fig. 1. *Diversity profiles of ground beetle (A) and rove beetle (B) assemblages with Rényi diversity index family. The solid line denotes recently established reforestation, the dashed line young reforestation, the dash-dot line middle-aged reforestation and the dotted line mature oak forest.*

lished and young reforestations. Forest specialist ground beetle assemblages of both the young and the middle-aged reforestations crossed the diversity profile of ground beetle assemblage of mature forest, therefore these cannot be unequivocally ordered (Fig. 2A).

There were no forest specialist rove beetles in the recently established reforestation, evidently resulted zero diversity (Fig. 2B). Diversity profiles of forest specialist rove beetle assemblages of the mature oak forest, the young and the middle-aged reforestations intersected to each other; therefore, these cannot be unequivocally ordered (Fig. 2B).

DISCUSSION

Diversity of ground beetles in reforestations

Clear-cutting and soil preparation before reforestation and the cultivation by light tilling during the management of the reforested stands cause many forms of disturbance, such as degradation, fragmentation and isolation of original habitats *(2).* In spite of dramatic alteration of mature forest stands our results showed that the diversity of ground beetle assemblages increased in the recently established reforestation. Similarly to our results several previous studies reported diverse ground beetle assemblages in recently established reforestation after 1–5 years of clear-cutting *(2, 33, 34).* In these studies the elevated diversity was explained by the colonization of open-habitat and habitat generalist species with high dispersal ability and the survival of some forest specialist ground beetle species *(2, 35).* However, other studies found that heavy site preparation after the clear-cutting (grubbing, tilling, deep loosening, burning) causes significant damage in ground beetle diversity in deciduous and coniferous non-native reforestations *(9, 12).* The reason for this is that heavy site preparation eliminates microhabitats required by the forest specialist species causing the disappearance of these species from the prepared, recently established

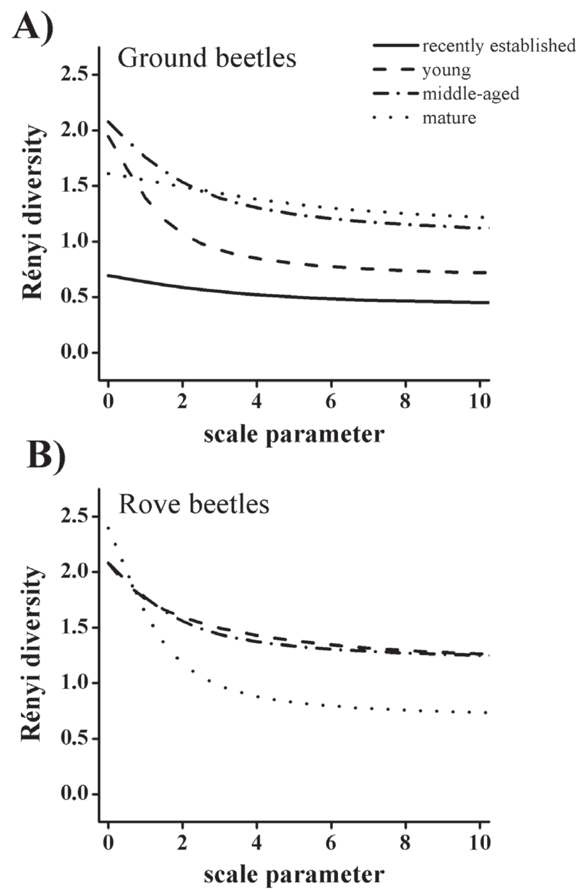

Fig. 2. *Diversity profiles of forest specialist ground beetle (A) and rove beetle (B) assemblages with Rényi diversity index family. There were no forest specialist rove beetles in the recently established reforestation; thus, the diversity profile of this assemblage is not displayed. The solid line denotes recently established reforestation, the dashed line young reforestation, the dash-dot line middle-aged reforestation and the dotted line mature oak forest.*

reforestations *(9)*. Moreover, reforestation with non-native tree species hampers the regeneration of favourable environmental conditions; thus, many native forest specialist species may not find their preferred habitat requirements even after 40 years of reforestation *(6, 9)*.

It has been shown that overall diversity is not the most appropriate indicator of the impacts of silvicultural cycle on surface-dwelling beetles *(2, 16)*. Instead of that, studies based on functional traits of the surface-dwelling beetle species are efficient approaches to follow this issue, and understand the requirements of specialist species *(2, 6, 15)*. Our findings suggest that clear-cutting of mature forest stands and reforestation with native tree species is not necessarily detrimental to ground beetle diversity, because early phases of reforestation (1–5 years after clear-cutting) provide habitat for species that are not present in the mature forest. These ground beetle species have high dispersal ability and ecological flexibility; therefore, they can colonize easily the reforested stands after some years of clear-cutting *(2, 35)*.

Although, the diversity of forest specialist assemblage reduced in the recently established reforestation, some forest specialist species could survive in these habitats. Thus, reforestation with native tree species resulted in high ground beetle diversity by colonization of good colonizer species from neighbouring habitats and survival of some forest specialist species in early phases of the reforestation. With canopy closure the diversity of ground beetle assemblages declined, while the diversity of forest specialist assemblages increased. Elevated forest specialist ground beetle diversity in later phases of the silvicultural cycle (after canopy closure) showed that clear-cutting and subsequent site preparation have a particularly harmful effect on forest specialist assemblages in the early phases of reforestation, as it was predicted by the habitat specialist hypothesis.

Diversity of rove beetles in reforestations

Reforestation with native tree species clearly affected the rove beetle diversity, as their assemblages were less diverse in younger reforestation than in the mature oak forest. Similarly, in Hungary the overall abundance and species richness of rove beetles were significantly lower in 40-year-old native reforestation and non-native plantations than in 135-year-old mature oak forest *(6)*. However, in China after 40 years of logging of climax forest, Luo et al. *(36)* found no significant differences in the rove beetle diversity between coniferous and deciduous reforestations and the control mature forest (≈100-year-old). Inconsistent results in rove beetle diversity were also found in previously published studies investigating forest succession *(13, 16, 34, 37)*. Our results demonstrated that total diversity of rove beetles is higher in later phases than in recently established reforestation. This result suggests that clear-cutting and soil preparation (grubbing, deep loosening) before reforestation and cultivation by light tilling during the forest management had detrimental effects on the rove beetle diversity in early phases of native oak reforestation. However, with ageing of the reforested stands the environmental conditions (temperature, soil moisture, pH) and habitat structure (closed canopy cover, native litter and woody debris) may become more similar to those of mature oak forest and the rove beetles can partially recover *(2, 6)*.

Almost all studies suggested that canopy closure and increasing similarity in structure, microhabitats and environmental conditions between the reforestations and the mature forests could be a key factor for some forest specialist species to recolonize the reforestations *(12, 16, 34, 38)*. In fact, the diversity of forest specialist rove beetles was lower in the recently established reforestation than in the young and middle-aged reforestations as well as the mature forest, in accordance with the hypothesized decrease of forest specialist species in highly disturbed (cultivated by light tilling) recently established reforestation *(17)*.

Study of rove beetles requiring specific microhabitat, microclimate and substrates may provide more details about the effects of forest management, since several microhabitats (nests, microcaves, deadwoods) and substrates (decaying fruits, litter, feces, fungi) are key components of biodiversity in forests *(1, 39)*. These components are eliminated during the intensive forest management, influencing the distribution of rove beetles requiring specific microclimate, microhabitats and substrates *(15)*. Nagy et al. *(6)* showed that the diversity of hygrophilous and decaying material dependent rove beetles were significantly higher in the mature oak forest than in the younger reforestations. Mature oak forest has more favourable microclimate, microhabitats and substrates for rove beetles requiring high soil moisture and decaying organic materials than reforestations *(1, 6)*. Presence of suitable microclimate, microhabitats and substrates contributes to the elevated rove beetle diversity in mature oak forest, while lack of those hampers the recovery of hygrophilous and decaying material dependent rove beetle species even after 40 years of reforestation *(6)*. Thus, despite of similarity in forest specialist's diversity between the later phases of silvicultural cycle (young, middle aged reforestations and mature forest) the rove beetles requiring specific microclimate, microhabitats and substrates may be a key contribution to increasing of rove beetle diversity in mature forest.

CONCLUSION

Our results demonstrated that ground beetles and rove beetles respond differently to reforestation with native tree species after clear-cutting of mature oak forest. The diversity of ground beetle assemblages was higher, while the diversity of rove beetles was lower in the recently established reforestation compared to that of mature forest. However, in case of both taxa the diversity of forest specialist assemblages showed consistent results, as diversity of the forest specialist species was lower in recently established reforestation than in mature forest. Most of the studies focus on overall species richness of arthropods, however some species may benefit and others suffer from the habitat alteration caused by forest management *(2)*. It is crucial to evaluate the effects of forest management on specialist species and try to find an alternative management practice which eliminate or reduce the harmful effects on biodiversity. Forest management treatments that do not alter drastically and permanently the environmental conditions, microhabitats and substrates could be appropriate methods in maintaining of the biodiversity. Therefore, we recommend that heavy site preparation (clear-cutting, grubbing, deep loosening) and management practices (light tilling) should be omitted during the reforestation and cultivation of the reforested stands in order to maintain the diversity of surface-dwelling beetles in managed forests. The uneven-aged management methods using selection cuttings have become more popular in Europe and it seems to be an appropriate method to maintain mature or late-successional forest characteristics and species assemblages *(2, 40–42)*.

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Appendix 1 *Collected ground beetle and rove beetle species and their classification based on works of Hůrka (1996) and Koch (1989) and also on our field experience in the stages of the silvicultural cycle.*

Species	Habitat affinity	Recently established	Young reforestation	Middle-aged	Mature forest
Ground beetles					
Acupalpus parvulus	open	-	-	+	-
Amara aenea	open	+	-	+	-
Amara bifrons	open	+	-	-	-
Amara convexior	forest	-	+	+	+
Amara familiaris	generalist	+	+	-	+
Amara fulva	open	+	-	-	-
Amara lucida	generalist	+	-	-	-
Amara ovata	forest	-	+	+	+
Amara saphyrea	forest	-	+	+	+
Amara tibialis	open	+	-	-	-
Badister bullatus	generalist	-	+	-	+
Bembidion lampros	forest	+	+	+	-
Bembidion quadrimaculatum	generalist	+	-	-	-
Calathus erratus	generalist	+	-	-	-
Calathus fuscipes	open	+	+	-	-
Calathus melanocephalus	generalist	-	+	-	-
Carabus convexus	forest	-	+	-	-
Harpalus distinguendus	open	+	-	-	-
Harpalus flavescens	open	+	-	-	-
Harpalus latus	generalist	+	+	+	-
Harpalus modestus	open	+	-	-	-
Harpalus picipennis	open	+	-	-	-
Harpalus pumilus	open	+	-	-	-
Harpalus smaragdinus	open	-	-	+	-
Harpalus tardus	open	+	+	+	-
Harpalus xanthopus winkleri	forest	+	-	+	-
Masoreus wetterhalli	open	+	-	-	-
Microlestes minutulus	generalist	+	-	-	-
Notiophilus palustris	forest	-	+	+	+
Notiophilus rufipes	forest	-	-	+	+
Ophonus rufibarbis	generalist	+	-	-	-
Oxypselaphus obscurus	forest	-	-	+	-
Parophonus complanatus	generalist	+	-	-	-
Philorhizus notatus	open	-	-	-	+
Platyderus rufus	generalist	-	+	-	-
Pseudoophonus griseus	open	+	-	-	-
Pseudoophonus rufipes	open	+	-	-	+
Pterostichus oblongopunctatus	forest	-	+	-	-
Pterostichus strenuus	generalist	-	+	+	-
Syntomus obscuroguttatus	generalist	+	-	+	+
Syntomus pallipes	open	+	-	+	-
Synunchus vivalis	open	-	+	-	+
Trechus quadristriatus	generalist	-	+	+	+
Rove beetles					
Alaobia scapularis	generalist	-	+	-	-
Aleochara bipustulata	generalist	-	-	+	-
Amauronyx maerkelii	no data	-	-	-	+
Amischa analis	generalist	+	-	-	-
Anthobium atrocephalum	generalist	-	+	+	+
Astenus procerus	open	+	-	-	-
Atheta benickiella	forest	-	-	+	+
Atheta euryptera	generalist	-	+	-	-
Atheta fungi	generalist	-	+	+	+
Atheta gagatina	forest	-	+	+	+
Atheta harwoodi	generalist	-	-	-	+
Atheta negligens	forest	-	-	-	+
Atheta orbata	generalist	+	-	+	+
Atheta voeslauensis	open	-	-	+	-
Batrisodes adnexus	no data	-	-	-	+
Bolitiobius castaneus	generalist	-	-	+	+
Bolitochara bella	generalist	-	-	+	+
Brachida exigua	open	-	-	-	+
Bryaxis carinula	no data	-	+	+	+
Bryaxis curtisii orientalis	no data	-	+	+	+
Carpelimus sp	no data	-	+	-	-
Cousya nigata	open	+	-	-	-
Dropephylla ioptera	generalist	-	-	-	+
Falagrioma thoracica	generalist	-	-	-	+
Gabrius osseticus	generalist	-	+	+	+
Geostiba circellaris	generalist	-	+	+	+
Gyrohypnus angustratus	generalist	-	+	-	+
Gyrophaena fasciata	forest	-	-	+	-
Gyrophaena joyioides	generalist	-	-	-	+
Habrocerus capillaricornis	generalist	-	-	+	+
Heterothops dissimilis	generalist	+	+	+	+
Ischnosoma splendidum	generalist	-	+	+	-
Lathrobium geminum	generalist	-	+	+	-
Liogluta granigera	generalist	-	-	-	+
Liogluta longiuscula	generalist	-	-	-	+
Lordithon thoracicus	forest	-	+	-	-
Medon fusculus	generalist	-	-	+	+
Metopsia similis	generalist	+	+	+	+
Mycetoporus eppelsheimianus	forest	-	+	+	+
Mycetoporus erichsonanus	generalist	-	+	-	+
Mycetoporus forticornis	generalist	-	+	-	-
Mycetoporus rufescens	generalist	-	+	-	-
Mycetota laticollis	generalist	-	-	+	-
Ocalea badia	generalist	-	+	+	+
Ocypus nitens	generalist	-	+	-	+
Omalium caesum	generalist	-	+	+	+
Omalium rivulare	generalist	-	-	-	+
Ontholestes haroldi	generalist	-	+	+	-
Othius punctulatus	generalist	-	+	+	+

Species	Habitat affinity	Recently established	Young reforestation	Middle-aged	Mature forest
Oxypoda abdominalis	generalist	-	+	+	+
Oxypoda acuminata	generalist	-	-	+	+
Oxypoda flavicornis	forest	-	+	-	+
Oxypoda opaca	generalist	-	-	+	-
Oxypoda togata	generalist	+	-	-	-
Oxypoda vicina	generalist	+	-	-	-
Pella laticollis	generalist	-	-	-	+
Pella ruficollis	forest	-	-	-	+
Philonthus concinnus	generalist	+	-	-	-
Philonthus succicola	generalist	-	+	-	-
Phyllodrepa melanocephala	forest	-	-	-	+
Pselaphus heisei	generalist	-	+	+	+
Quedius curtipennis	generalist	-	+	-	+
Quedius fuliginosus	generalist	-	-	-	+
Quedius limbatus	forest	-	+	+	+
Quedius scintillans	generalist	+	-	-	+
Rabigus pullus	generalist	+	-	-	-
Rugilus rufipes	forest	-	-	+	+
Rugilus subtilis	generalist	-	-	+	-
Scaphidium quadrimaculatum	forest	-	+	-	+
Scaphium immaculatum	generalist	-	+	+	-
Scopaeus pusillus	open	+	-	-	-
Sepedophilus immaculatus	generalist	-	+	-	-
Sepedophilus marshami	generalist	-	+	+	+
Sepedophilus obtusus	generalist	+	+	+	-
Sepedophilus pedicularis	generalist	-	+	-	-
Sepedophilus testaceus	generalist	-	-	+	+
Stenus ater	open	+	+	-	-
Stenus clavicornis	open	+	+	-	-
Stenus humilis	forest	-	+	+	-
Stenus ludyi	forest	-	+	+	+
Stenus ochropus	generalist	+	+	+	+
Sunius fallax	generalist	+	+	+	+
Tachinus fimetarius	generalist	-	-	-	+
Tachyporus atriceps	generalist	-	-	-	+
Tachyporus chrysomelinus	generalist	-	-	+	-
Tachyporus hypnorum	generalist	+	+	+	+
Tachyporus nitidulus	generalist	-	+	+	+
Tasgius morsitans	generalist	-	-	-	+
Thinonoma atra	generalist	-	-	-	+
Xantholinus longiventris	generalist	-	+	-	-
Zyras collaris	generalist	-	-	+	-
Zyras haworthi	generalist	-	-	-	+