

Functional plasticity of carabids can presume better the changes in community composition than taxon-based descriptors

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Abstract. Although the functional trait approach can facilitate the understanding of mechanisms that underline community responses to habitat alteration, only a few studies used this way on exploring the structure of insect assemblages compared to taxon-based analyses. We compared the descriptive power of medium-term effects (2014–2018) of forestry treatments in a temperate managed oak-dominated forest on taxon- vs. trait-based descriptors of ground beetle assemblages. The treatments included rotation forestry (partial preparation cutting, clear-cutting, retention-tree group, and mature closed forest as control) and continuous cover forestry (gap cutting) operations. The species composition was only slightly influenced by the treatments; on the ordination biplot, the control, retention tree group, and clear-cutting treatments formed relatively homogeneous groups, well separated from each other, while the others were scattered randomly in the ordination space. Over time, the species richness decreased in all treatments, but it was higher in the retention tree group treatment than in others in 2016 and 2017. The activity density also declined between years, but an immediate mass effect was revealed after the implementation of treatment types especially in the control, gap, and preparation cuts. We found that assemblages in the clear-cutting and retention-tree group had similar characteristics: high functional diversity; more open-habitat, generalist, and omnivore species and fewer carnivore species; while those in the control, gap, and preparation cutting groups had the opposite: lower functional diversity, more forest species, and more carnivorous species. Our findings will demonstrate that the simultaneous use of the two approaches will allow the most articulate understanding of the status of ground beetles assemblages in managed forests.

Key words: forest management; functional diversity; functional traits; ground beetles; temperate deciduous forests.

INTRODUCTION

Forest ecosystems are important to mitigate the unfavorable effects of global climate change through their potential to influence local climatic conditions and their crucial role as a global carbon stock (Horák et al. 2019). Although the historical overexploitation of European forests considerably changed their structure and composition (Kaplan et al. 2009), currently the importance of conservation, climate change mitigation, and recreational services are increasing compared to wood production (Mori et al. 2017). An ecologically sustainable forest management also demands better understanding of the environmental drivers of assemblage composition

and diversity across taxonomic groups to ensure the multifunctionality of forest ecosystems (de Groot et al. 2016, Sitzia et al. 2017). In this changing milieu, European forestry is shifting toward the so called “close-to-nature” forestry (Bauhus et al. 2013), mimicking the natural disturbance regime to support biodiversity and ecosystem functioning of forests (Kuuluvainen and Aakala 2011, Koivula et al. 2019). There are many approaches within this forestry framework including management maintaining old-growth attributes (Bauhus et al. 2009), continuous cover forestry (Pommerening and Murphy 2004), and green-tree-retention forestry (Mori and Kitagawa 2014).

To compare the effect of different forest management approaches on biodiversity, we studied the response of ground beetles to site conditions modified by silvicultural practices. Ground-dwelling predatory arthropods such as carabids (Coleoptera: Carabidae) are good indicators of the effects of various forest managements

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(Niemelä et al. 2007). This group has a relatively short generation time (Thiele 1977, Lövei and Sunderland 1996) and a relatively high position in the food web (Wootton 1998) allowing for a complex response to changes in their abiotic and biotic environment. Their assemblage composition is very sensitive to structural complexity of forest stands at different temporal and spatial scales (Niemelä et al. 2007, Negro et al. 2008).

Within the framework of biodiversity and conservation studies in managed forests, species composition, richness, alpha diversity indices, and abundance are the simplest measures for biodiversity, based on the species taxonomic identity of the individuals (Magura 2017). Previous studies revealed that species composition have changed the most, while changes in species richness and abundance among forestry treatment were equivocal, mostly connected to the annual variation (Heikkala et al. 2016, Koivula et al. 2019, Yamanaka et al. 2021). Changes in the taxon-based measures for ground beetle assemblages will evidently reflect carabids' functional role in the forest ecosystems due to the fact that their functional traits are highly connected with their taxonomic identity (Magura 2017, Magura and Lövei 2019). The inclusion of species' functional traits often appears with the premise of exploring the resources utilization, dispersal, or reproduction. Schirmel et al. (2012) revealed that functional traits may contribute to trait-based environmental filtering in forming species communities. Although functional traits analysis can indirectly estimate the ecosystem functions, its use is more suitable to the species' population level (Murray et al. 2017). In theory, functional diversity metrics can be used for exploring the effects of disturbance on community level processes and changes in ecosystem function (Botta-Dukát 2018). With standardized methods for functional diversity, previous investigations (Schirmel et al. 2012, Murray et al. 2017, Nolte et al. 2017) have recently assessed the functional diversity responses to disturbance in various forested habitats and taxonomic groups. These studies revealed that the functional diversity of an assemblage represents a direct link between the environment and emergent ecosystem functions and can be taxon dependent. Furthermore, Murray et al. (2017) also added that functional diversity cannot be assumed to have positive covariance with species richness due to functional redundancy, where multiple species perform similar roles in an ecosystem. However the proper use of functional trait and diversity measures on the impact of forest management types still needs to be clarified (Spake et al. 2016, Nolte et al. 2017).

In a randomized block experiment, we investigated the medium-term (up to four years after the implementations) effects of four forestry treatments related to rotation (Matthews 1991) and continuous cover forestry systems (Pommerening and Murphy 2004) on ground beetles. Our major aims were to (1) explore how the taxon-based descriptors of carabid assemblages

(composition, species richness, diversity, and abundance) vs. functional trait-based descriptors (functional diversity, groups based on habitat affinity, wing morphology, and feeding guilds) respond to the different forestry treatments; (2) identify the combination of functional traits of ground beetles that the most sensitively indicate the effects of different forestry treatments and thus can serve as indicators when seeking an ecologically sustainable forest management.

With reference to the first question, we expected that species richness, abundance, and diversity are more sensitive to between-year variation and structural changes of beetle assemblages in time. With reference to the second question, we expected that the higher functional diversity of clear-cuts and retention-tree groups is related to the invasion of habitat generalist and open-habitat species with high dispersal power, which causes a decline in the population of true forest-dwelling carabids with weak dispersal ability. Our findings will elucidate that the simultaneous use of taxon and trait-based approaches will provide the most articulate understanding of the status of ground beetles assemblages in response to forestry management.

METHODS

Study area

The study area is located in the Pilis Mountains (47°40' N, 18°54' E), in the northern part of Hungary in southeastern Europe (Fig. 1). The hills are at elevation of 370–470 m above sea level, with an annual precipitation of 600–650 mm and a mean annual temperature of 9.0–9.5°C (Dövényi 2010). The bedrock of the area is limestone and red sandstone with loess deposits, forming a luvisol type soil (Krasilnyikov et al. 2009). The investigated 40-ha stand was an even-aged mature (80 yr old) oak–hornbeam forest (Natura 2000 code: 91G0, European Commission 1992). The stand has been managed by shelterwood silvicultural system (Matthews 1991), where the height of the upper canopy layer at 21 m was dominated by sessile oak (*Quercus petraea* (Matt.) Liebl., height 21 m, diameter at breast height 28 cm), and a secondary canopy at 11 m contained mainly hornbeam (*Carpinus betulus* L.). Less common tree species included turkey oak (*Quercus cerris* L.), beech (*Fagus sylvatica* L.), wild cherry (*Prunus avium* L.), and manna ash (*Fraxinus ornus* L.). The shrub layer was scarce; and ground cover was 30%, with *Carex pilosa* Scop. and *Melica uniflora* L. as dominant herbs.

Experimental design

Our study plots belonged to the Pilis Forestry Systems Experiment, which studies the effect of different forestry treatments on forest site, biodiversity, and regeneration (<https://piliskiserlet.ecolres.hu/en>). We established five forestry treatments using a complete block design with

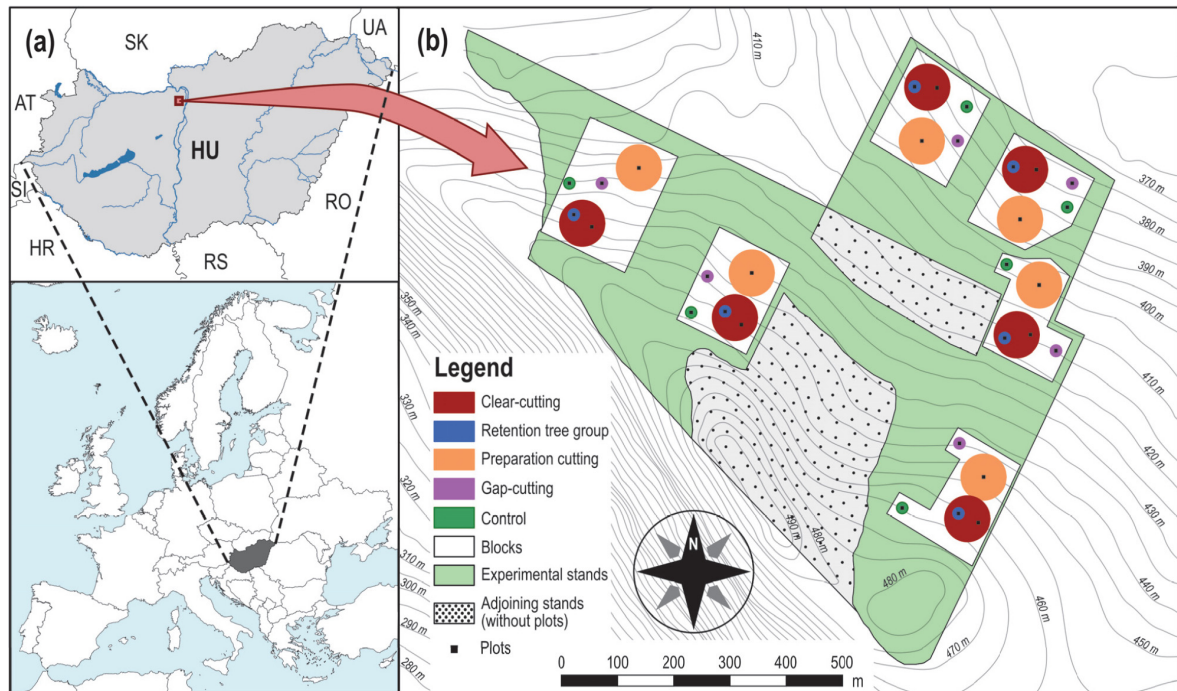


FIG. 1. (a) Map of the study area in the Pilis Mountains, Hungary and (b) the design of the Pilis Forestry Systems Experiment. Countries are HU, Hungary; SK, Slovakia; UA, Ukraine; RO, Romania; RS, Serbia; HR, Croatia; SI, Slovenia; AT, Austria.

six blocks as replicates (Fig. 1). Treatments were control (C), a mature, closed-canopy stand without any treatment; clear-cutting (CC), all trees cut and removed from a circular area of 80 m diameter (0.5 ha); gap-cutting (G), a circular gap in the closed stand (20 m diameter, tree-height: plot-diameter ratio ~ 1); preparation cutting (P), 30% of the total basal area of the upper canopy trees and the whole secondary tree layer cut in a circle of 80 m diameter; and retention-tree group (R), a circular group of upper canopy trees (20 m diameter, 8–12 dominant individuals, untouched sub-canopy layer) was retained in the clear-cutting. Control, clear-cutting, retention-tree group, and preparation cutting represent characteristic stages of rotation forestry system, while gap-cutting is often implemented in the framework of continuous cover forestry (selection forestry system). The treatments were established during the winter of 2014–2015. The resulting 30 plots (5 treatments \times 6 replicate blocks) were treated as basic sampling units.

The microclimate and soil conditions have been continuously monitored as a part of the project (Kovács et al. 2020). After the first three years, clear cuts were characterized by increased mean and variability of air and soil temperatures. Retention-tree groups could effectively ameliorate the temperature extremes but not the means. Preparation cuts induced slight changes from the original buffered forest microclimate. Despite the substantially more incoming light, gaps could keep the cool

and humid air conditions and showed the highest increase in soil moisture after the interventions.

Data collection

Data collection followed the concept of Before-After Control-Impact experiments (Green 1979), recording all investigated variables from the vegetation period of 2014 (before the implementation) until 2018. Four pitfall traps were installed in every plot in the nodes of a 5-m grid to sample ground beetles. Each year, the community was sampled in spring (June) and autumn (September) for one month corresponding to the highest activity regime of the beetles (Sapia et al. 2006). The traps were made of 85 mm diameter plastic cups; each containing approximately 250 cm³ of a 50% solution of propylene glycol and water, saturated with salt, and with a drop of odorless detergent to reduce surface tension. A dark green plastic roof protected the solution from litter and rain. For identification, keys by Lindroth (1985, 1986) and Hürka (1996) were used and taxonomy follows Hürka (1996). The activity density data of the four pitfall traps of the same plots were merged, thus the elementary sampling units of the analyses were the plots. The term activity density refers to the empirical fact that catches of pitfall traps depend on the individuals' activity; the higher activity of the individuals, the more catches in the traps. Although this term is the most

accurate proxy for such data, the most common one is the abundance, thus we used this term hereafter.

Analyses

We conveyed the following analyses at two main foci, including the taxonomical and functional approaches to explore whether the effect of forest management on carabids are the results of temporal/random variation in collection of species or the consequence of consistent changes in ecosystem functions (*sensu* Cadotte et al. 2013). In all analyses, the effects of the applied five treatments and years (from 2015 to 2018) were analyzed on the different response variables of ground beetle assemblages.

In the taxonomical approach, the effect of treatments on species composition was explored by Principal Component Analysis (PCA) with a square-root transformation for investigating the separation of treatments in different years, as well as the relationships between species composition and treatments (Venables and Ripley 2002). The separation of the treatments was statistically tested by Permutational Multivariate Analysis of Variance (PERMANOVA) using Euclidean distance. The species associations to treatments were confirmed by the Indicator Value Analysis (IndVal) method (Dufrene and Legendre 1997). We considered a species as characteristic for a particular treatment type when both the ordination (PCA) and IndVal revealed its association to that treatment. All of the analysis of species composition (PCA, PERMANOVA, IndVal) were carried out for each year separately.

The diversity of an assemblage is based on the species taxonomic identity weighted by its abundance in the assemblage. In the case of the Rényi one-parametric diversity index family, not just one numerical value is used to characterize the diversity of an assemblage, but a family of diversity values (Tóthmérész 1995). This method can be used in a graphical form to visualize the diversity relationships of assemblages (Lövei 2005). Members of the one-parametric diversity index family have varying sensitivities to rare and abundant species as the scale parameter changes (Tóthmérész 1995). Scale parameter 0 is equivalent to log-transformed species richness, 1 to Shannon, 2 to Simpson diversity, while high parameters are equivalent to the Berger-Parker dominance index.

During the evaluation of functional approach, traits related to body size, wing morphology, breeding season, overwintering stage, feeding preference, and habitat affinity were collected for each species (Appendix S1: Table S1) using the available literature (Thiele 1977, Lindroth, 1985, 1986, Laroche 1990, Hürka 1996, Turin et al. 2003). The final list of the assessed functional traits were habitat preference (forest specialists, open-habitat species, and generalists), wing morphology (brachypterous, macropterous), and feeding preference (carnivores, omnivores) due to data saturation. These functional

differences between species in a community cannot be described quantitatively by traditional diversity measures (Botta-Dukát 2005). Several functional diversity indices are available, the most common measures assume that within and between group differences are equal and ignore the abundance of the characterized group (Mason et al. 2003, Botta-Dukát 2018). Botta-Dukát (2005) proposed an index (FD_Q or Rao's Q) based on the quadratic entropy of Rao (1982), which consider the relative abundances of the species and measures for the pairwise functional differences between species. One of the major advantages of Rao's Q is that it can handle the species abundances and many traits (Loreau 2001, Botta-Dukát 2018), thus we applied this index to characterize the functional diversity for management types and years.

We built generalized linear mixed models (GLMMs) to separate the effect of the two analytical foci. The effect of treatments and years and their interactions (considered as a fixed effect terms) were tested on the set of response variables, while blocks were used as a random factor to consider the spatial replicates. In GLMMs, species richness and abundance per plot were used as response variables in the taxonomical approach, while the calculated Rao's Q values and the abundance of selected functional groups were considered in the functional approach (Appendix S1: Table S1). Two families of distribution were applied, Poisson and Gaussian, to ensure the best fit of the tested data on abundance at all measures and on expected values of species richness and functional diversity by Rao's Q , respectively. The models were tested with the default Laplace approximation to the log-likelihood. The model diagnostics include the inspection of model residuals' structure (Pearson's type) vs. fitted values and degrees of freedom either in the model's output or in graphs. In case of significant treatment effects, the differences between treatment levels were evaluated by multiple comparisons with Tukey computed contrast matrices for several multiple comparison procedures.

All analyses were carried out in R 3.6.3 (R Core Team 2020); using the package *vegan* (Oksanen et al. 2019) for PCA (function *rda*), for PERMANOVA (function *adonis*), and for Rényi diversity (function *renyi*). The package *labdsv* (Roberts 2019) was used for IndVal calculations (function *indval*), package *FD* (Laliberté and Legendre 2010, Laliberté et al. 2014) for calculating Rao's Q functional diversity index (function *dbFD*), *lme4* (Bates et al. 2013) for GLMM (function *lmer*), and *lsmeans* (Lenth 2016) with *multcompView* (Graves et al. 2019) for multiple comparisons (functions *lsmeans* and *clt*).

RESULTS

Assemblage characteristics

During this study, we collected 21,352 individuals of 49 species. *Carabus hortensis*, *Abax ater*, *Carabus scheidleri*, *Aptinus bombardaria*, *Carabus ullrichi*, *Carabus*

coriaceus, *Nebria brevicollis*, *Pterostichus melanarius*, *Carabus nemoralis*, *Calathus fuscipes*, *Aptinus parallelus*, *Carabus cancellatus*, *Carabus convexus*, *Molops piceus*, and *Pterostichus oblongopunctatus* constituted 97% of the total capture. The majority of the dominant species were forest-associated species (10 out of 15), four species were habitat generalists, while only one species was an open-habitat specialist (see Appendix S1: Table S1 for details). In 2014, there were no differences between the sampled assemblages in the area of the planned, but not yet implemented, treatments (Appendix S1: Fig. S1–S4).

Assemblage composition and species–treatment associations

The PCA analyses revealed that, after the implementation of treatment types in early 2015, the carabid assemblages occupying the retention-tree groups and clear-cuts formed a distinct group, while other treatments formed another one; a similar trend was revealed in 2016. The control plots became distinct from all other treatment types in 2017 and 2018 (Fig. 2). The greatest separation between the treatments was found in the third year (2017) of the experiment. The species associated with the studied treatments showed treatment-specific

variation between years (Fig. 2); *A. bombarda* was associated with control forests in all studied years; *A. ater* and *C. hortensis* were also control-associated species but only in 2016. In the clear cuts, *Pseudophonus rufipes* and *Carabus granulatus* were characteristic species in the first two years of the study (2015–2016), while *C. coriaceus* was the only species associated with clear cuts in 2017. In 2018, *P. melanarius* and *C. scheidleri* became associated with clear-cuts. *Nebria brevicollis* was associated with gaps in 2015, while in 2017 it was *A. ater*. *Carabus convexus* was characteristic species for retention-tree groups in the first two years of the study; while *C. fuscipes* became associated with this treatment in 2016 and 2017. *Laemostenus terricola* and *Notiophilus rufipes* were also characteristic for retention-tree groups in 2015 and 2017, respectively. *Carabus coriaceus* in 2016, while *C. nemoralis* in 2017 were the species associated with preparation cuts.

Diversity, species richness, abundance

Rényi diversity profiles showed a particular variation in alpha diversity between treatments and years. Immediately after the implementation of the forestry treatments in 2015, the species richness estimated by Rényi

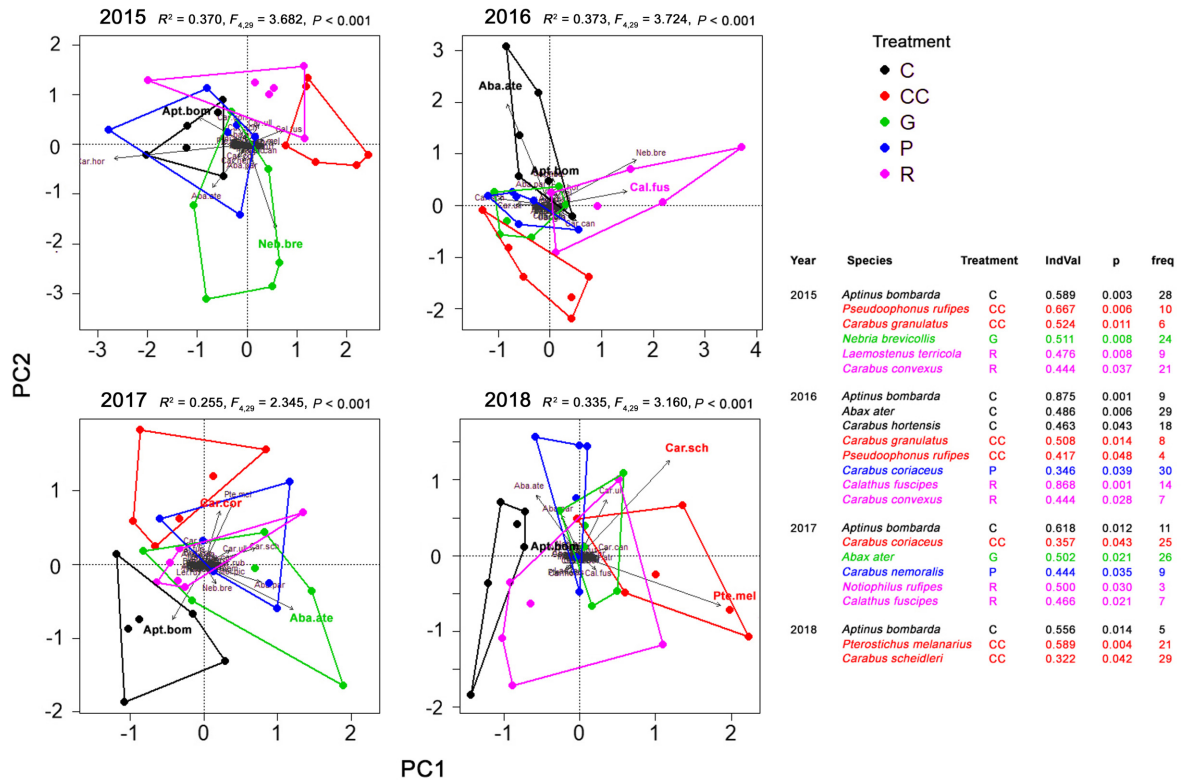


FIG. 2. Biplot for principal component (PC) analyses on the abundance of the ground beetles. The compositional difference between treatments expressed as the results of the PERMANOVA (coefficient of determination, *F*, and *P* values) are portrayed on each graph panel. The table on the right summarizes the maximal indicator values of species and their significance to treatments based on the IndVal method. Only significant results (*P* < 0.05) are shown. The treatments are control (C, black), clear-cutting (CC, red), gap-cutting (G, green), preparation cutting (P, blue) and retention-tree group (R, purple).

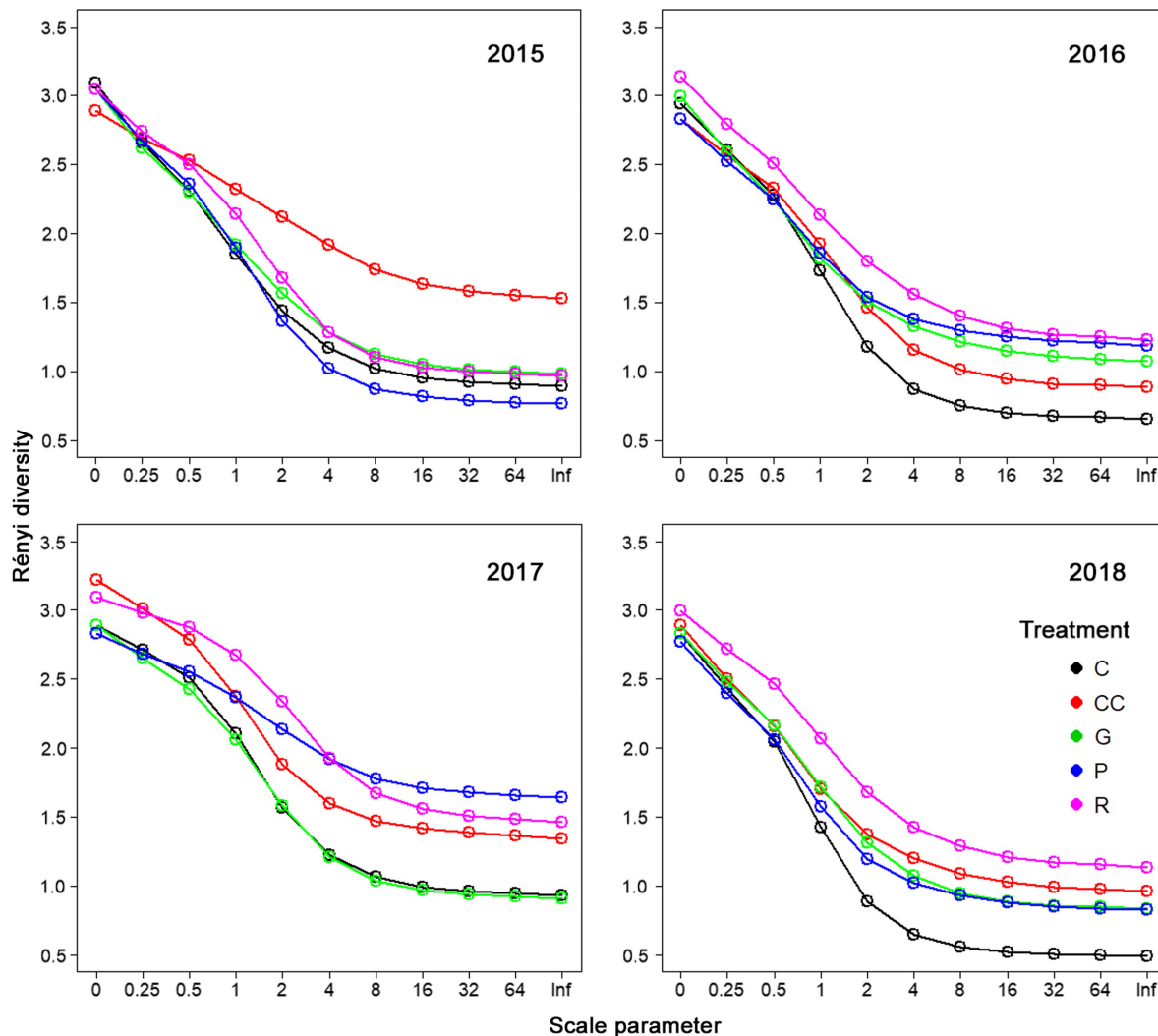


FIG. 3. Diversity profiles of carabid assemblages in different forestry treatments and years by the Rényi diversity. The abbreviations and colors of the treatments are the same as in Fig. 1.

diversity at scale parameter 0 (Fig. 3) was the lowest in the clear-cuts, while the diversity indices sensitive to the dominant species (scale parameter > 64) were the highest in this treatment. In 2016, the retention-tree group was consistently the most diverse treatment type based on the whole range of the scale parameter. In the third year (2017), diversity profiles were inconsistent between the treatment types; the species richness (at scale parameter zero) was the highest in the clear-cuts and, retention-tree groups, while preparation cuts had the highest diversity at high values of the scale parameter. In addition, the diversity was consistently the lowest in gap and control treatments in 2017. In 2018, the diversity was unequivocally the highest in the retention-tree groups and lowest in control (Fig. 3).

The overall species richness and abundance of carabids decreased in consecutive years; treatment effect revealed a year-specific change for both measures

(Table 1; Fig. 4). For species richness, the effect of treatments was modest and had a significant effect only in 2016. This year, it was the highest in the retention-tree groups and the lowest in the clear-cuts; other treatments had intermediate positions. For abundance, an immediate mass effect was revealed after the implementation of treatment types. In 2015, most individuals occurred in preparation cuts, control, and gap cuts, and the retention-tree groups and clear-cuts hosted the fewest individuals. Later, the patterns became inconsistent: in 2016, the control and retention-tree groups had the highest, while in 2018, they had the lowest abundance values.

Functional diversity and functional group responses

For functional diversity (Rao’s Q), the effect of treatments and years had a similar influence. In all years, it was the highest in the clear-cuts and retention-tree

TABLE 1. Summary of the linear mixed effects models for all studied response variables of ground beetle assemblages in the Pilis Mountains, Hungary

Group and variables	χ^2	df	<i>P</i>	Comparisons
Species richness†				
Treatment	16.778	4	0.002	R > CC
Year	141.568	3	<0.001	2015 > 2016 > 2017 = 2018
Treatment × Year	20.962	12	0.051	
Abundance, N_{\ddagger}				
Treatment	320.62	4	<0.001	P = G > R = C > CC
Year	7,663.91	3	<0.001	2015 > 2016 > 2018 > 2017
Treatment × Year	438.77	12	<0.001	
Functional diversity, Rao's Q_{\ddagger}				
Treatment	61.984	4	<0.001	CC > P = C, CC > G, R > P = C
Year	53.768	3	<0.001	2017 > 2015, 2017 > 2018
Treatment × Year	15.133	12	0.234	
Forest species, N_{\ddagger}				
Treatment	1,064.26	4	<0.001	C > G, C > R, C > CC
Year	7,750.17	3	<0.001	2015 > 2016 > 2018 > 2017
Treatment × Year	137.19	12	<0.001	
Generalists, N_{\ddagger}				
Treatment	220.54	4	<0.001	CC > R = G = P > C
Year	811.68	3	<0.001	2015 = 2016 > 2018 > 2017
Treatment × Year	278.65	12	<0.001	
Open-habitat species, N_{\ddagger}				
Treatment	371.478	4	<0.001	R > CC > P = G = C
Year	216.163	3	<0.001	2015 > 2016 > 2017 = 2018
Treatment × Year	60.844	12	<0.001	2016
Brachypterous species, N_{\ddagger}				
Treatment	395.56	4	<0.001	P > G, P > C, P > R, P > CC, G > R, G = C > CC
Year	7,222.03	3	<0.001	2015 > 2016 > 2018 > 2017
Treatment × Year	411.96	12	<0.001	
Macropterous species, N_{\ddagger}				
Treatment	277.63	4	<0.001	R > C, R > P, G > C, G > P
Year	555.46	3	<0.001	2015 > 2016 > 2017 > 2018
Treatment × Year	321.29	12	<0.001	
Carnivores, N_{\ddagger}				
Treatment	595.57	4	<0.001	P ≥ G ≥ C > R > CC
Year	7,863.2	3	<0.001	2015 > 2017
Treatment × Year	260.18	12	<0.001	2015
Omnivores, N_{\ddagger}				
Treatment	400.917	4	<0.001	CC = R > P = G > C
Year	56.231	3	<0.001	2015 > 2017
Treatment × Year	224.495	12	<0.001	

Notes: Significant effects are shown in boldface type and Tukey multiple comparisons for treatment types and years are designated by relation signals, where the “≥” designate the subsetting or partial differences among treatment types. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P), and retention-tree group (R).

† Gaussian.

‡ Poisson.

groups (Table 1; Fig. 4). When species were grouped by their habitat affinity types, there was a strong treatment and between-year variation, suggesting the overall decline of carabids during the years (Table 1; Fig. 5). The abundance of forest species was highest in the control, intermediate in gap and preparation cutting, and lowest in clear-cutting and retention-tree group but only in the first two years. The treatment differences decreased in 2017 and 2018. The abundance of generalists was consistently higher in all treatments than in the

control. The abundance of open-habitat species was the highest in the retention-tree groups, followed by the clear-cuts and preparation cuts, while open-habitat species were least abundant in the gaps and the controls.

The wing morphology types showed contrasting responses for the various treatments (Table 1; Fig. 6). Brachypterous species were the most abundant in preparation cuts and controls followed by gaps and retention-tree groups, while clear-cuts had the lowest abundance for this group. This trend was most evident in 2015 and

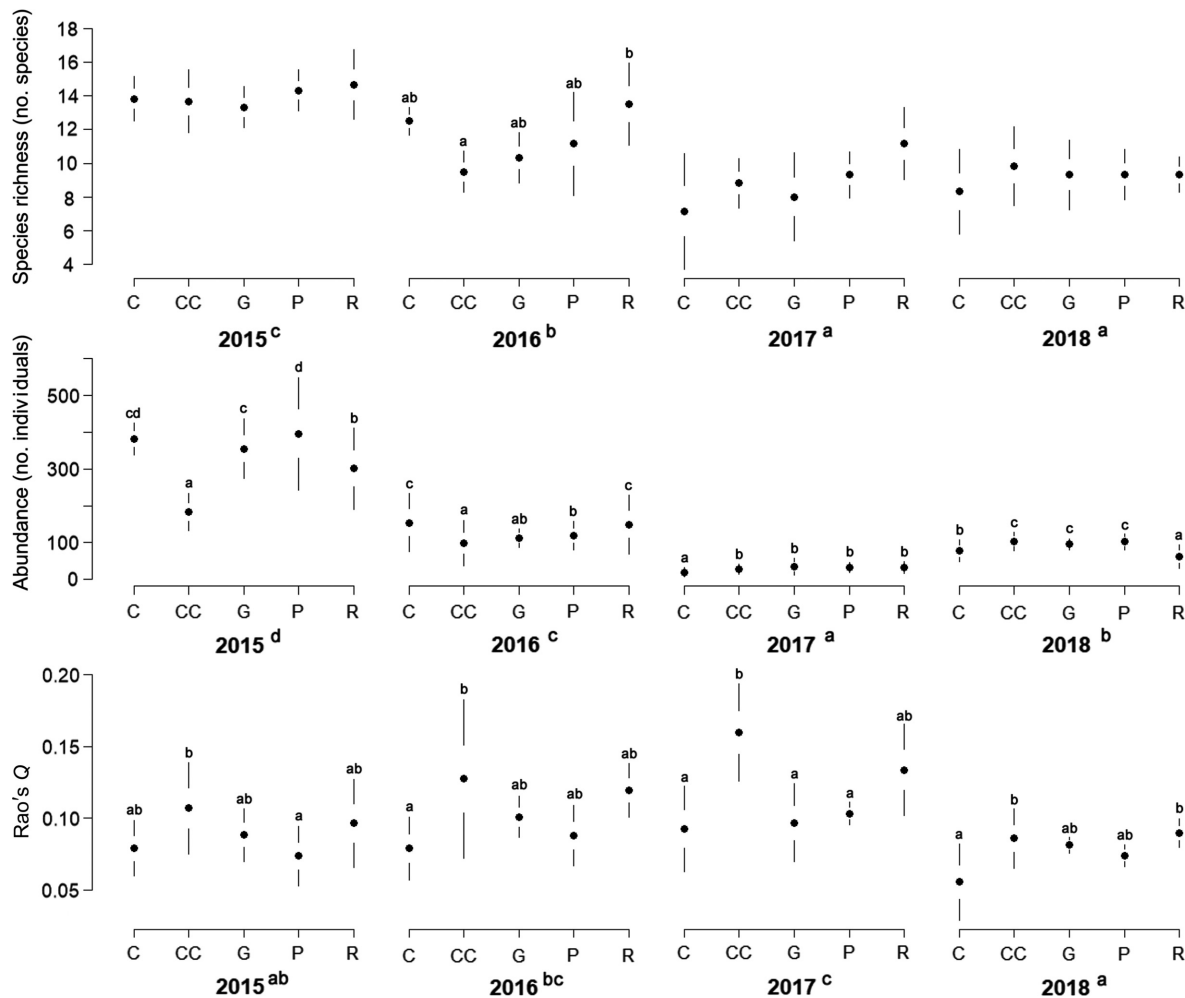


FIG. 4. Response of carabids' species richness, abundance, and Rao's Q to forestry treatments and years. Full circles show the mean, white space between the circles and the lines shows the standard errors of the mean, and vertical lines denote the standard deviations. Different lowercase letters designate significant differences among treatments and years; significance level was set at 0.05. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P), and retention-tree group (R).

became less distinct over the years. Macropterous species were most abundant in gap in 2015, in retention-tree group in 2016, while no considerable differences among the treatments were found in the last two years.

The assemblages, when was sorted on the basis of feeding habits, showed similar responses as in the case of wing morphology (Table 1; Fig. 6). The abundance pattern of carnivorous species was the same as those of the brachypterous species, suggesting the preference for more closed habitats such as preparation cuts and controls (Table 1). The omnivorous species showed the opposite trend and were the most abundant in more open habitats such as retention-tree groups and clear-cuts.

DISCUSSION

We conclude that the clear-cutting and retention-tree group had the most profound effect on carabid

assemblages, either on the basis of taxonomical or functional characteristics. We found high functional diversity characterized by mostly omnivorous, open-habitat, and generalist species within these treatments. We detected the opposite patterns in more closed habitats (control, gap, and preparation cutting) characterized by low functional diversity, with the high abundance of forest species and carnivores. These congruencies between functional responses can underline the fact that species traits can shape the assemblage composition especially in the medium-term responses for forestry treatments.

Taxonomical measures reflect between-year differences and variation in assemblage composition

Species composition showed the high variation between years and treatments, the major finding being that the closed forest is not subject to any forestry operation remained distinct from all other treatments over the

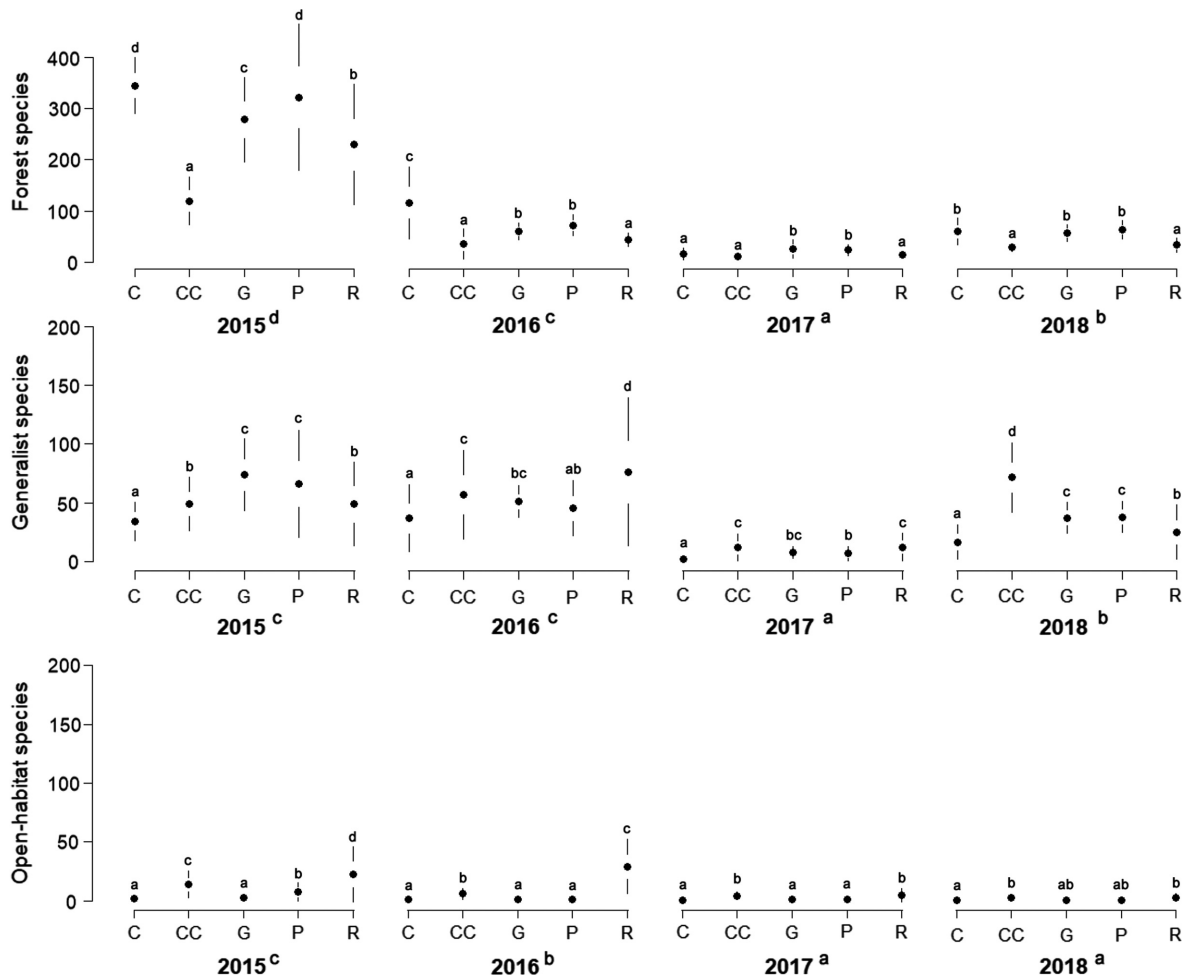


FIG. 5. Response of activity density of carabids' habitat affinity groups to forestry treatments and years. Full circles show the mean, white space between the circles and the lines shows the standard errors of the mean, and vertical lines denote the standard deviations. Different lowercase letters designate significant differences among treatments and years; significance level was set at 0.05. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P), and retention-tree group (R).

four years, suggesting that the recovery of carabid assemblages has not yet started. This is congruent with Koivula et al. (2019), where the carabid assemblages remained different after 10 years of the forestry intervention. The considerable variation of species composition between treatments and years suggest that seasonal variation in activity can appear even in closed forests, as in our study (Heikkala et al. 2016, Pinzon et al. 2016, Koivula et al. 2019). This high variation also reflected in the alpha diversity pattern between treatments. After the implementation treatment types that resulted more open environment, in the clear-cuts and retention-tree groups and those were the most diverse over years. This pattern can be explained by the fact that early successional carabid assemblages may have long-term founder effect that governs the future assembly composition (sensu Weslien et al. 2011, Heikkala et al. 2016). In addition, carabid assemblage composition of control mature forest can be

strongly influenced by the long-term forestry and land-use history resulting in the decline of forest specialists in the forested landscape (Magura 2017, Elek et al. 2018).

Functional traits reflect better treatment effects and are less sensitive for annual variation than taxon-based descriptors

The Rao's *Q* showed a consistent pattern between treatments over the years, suggesting that the wide range of available functional traits improved in the more open habitats, such as clear-cuts and retention-tree groups, while the control forest seems the least diverse in terms of functional traits for carabid assemblages. This pattern can be explained by the presence of open-habitat and generalist species in the more open habitats and their occurrence remains consistent over the years. Koivula et al. (2019) for carabids and Pinzon et al. (2016)

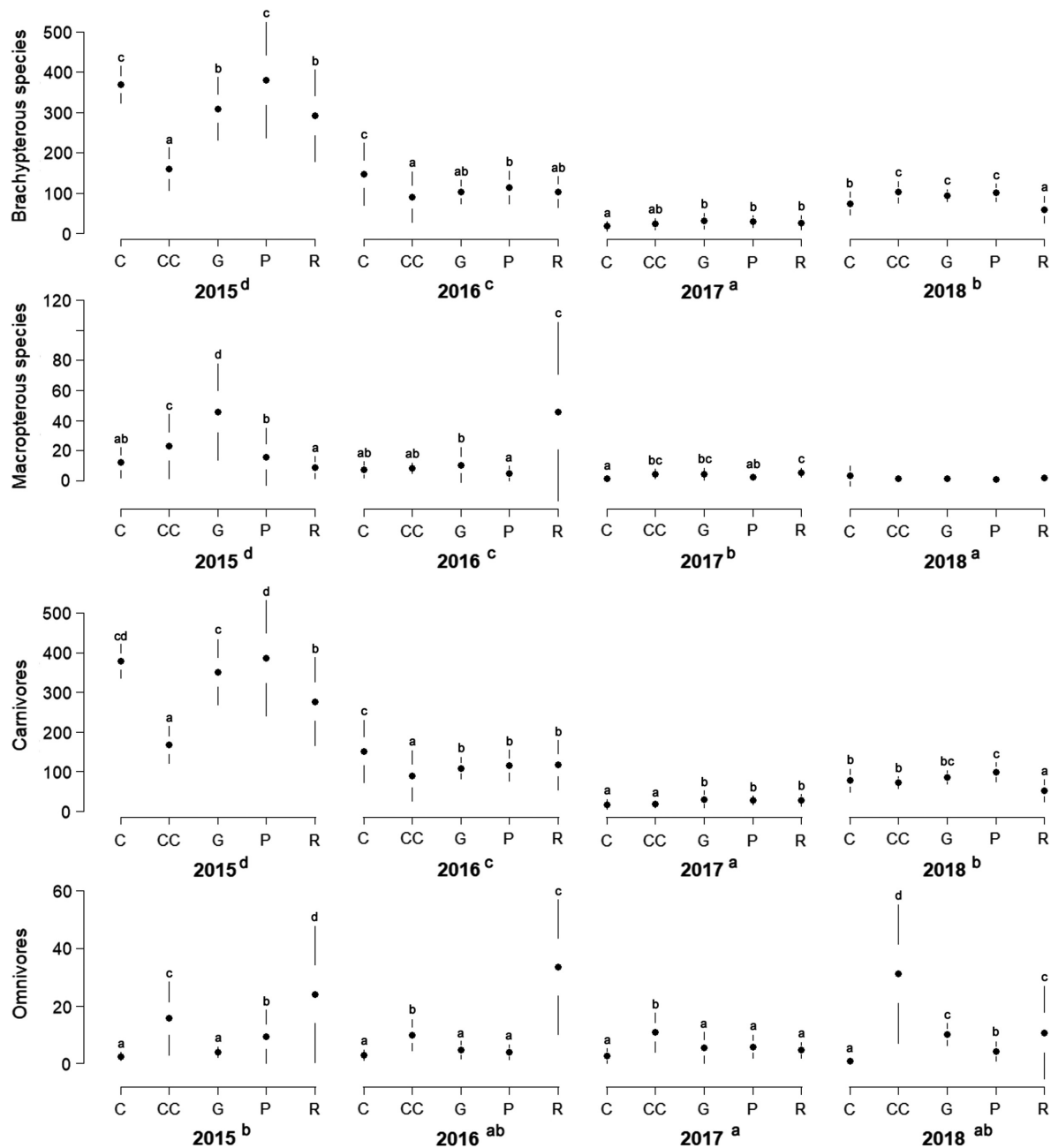


FIG. 6. Response of activity density of carabids' wing morphology and feeding preference types to various forestry treatments and years. Full circles show the mean, white space between the circles and the lines shows the standard errors of the mean, and vertical lines denote the standard deviations. Different lowercase letters designate significant differences among treatments and years; significance level was set at 0.05. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P), and retention-tree group (R).

for spiders, found similar patterns in boreal forests after 10 years of forestry treatments. In addition, our findings also support the hypothesis that carabid assemblages were randomly organized from the original forest carabids and the newly colonizing open-habitat and generalist species. Omnivorous species was more abundant in the clear-cuts and retention-tree groups together with

carnivorous species of moderate abundance. Heikkala et al. (2016) have found comparable responses, where the complex assessment of saproxylophagous beetles showed similar functional trait patterns in clear-cuts, suggesting that there is no clear resource utilization in more open habitat types. Similar patterns were also detected for dispersal ability: the abundance of brachypterous species

was higher in the more closed habitats (control and preparation cuts) in the first two years of the study, whilst the abundance of macropterous species was inconsistent showing the random arrival of carabids to the more opened habitat in the first two years. These patterns can be explained by the presence of dimorphic species where wingless (brachypterous) and winged (macropterous) forms can co-occur. The winged form of these species has higher colonization ability and can arrive in the early stages of succession (Kotze and O'Hara 2003), while the wingless individuals can support the assemblage persistence under stable habitat conditions (Nolte et al. 2017). This is congruent with the low functional diversity in control plots (i.e., closed forests), suggesting that the available functional space, in terms of the ecological niche concept, are already held mainly by carnivorous forest specialist carabids with low dispersal capacity (Nolte et al. 2017). The relatively homogeneous forest stand with closed canopy can prevent the establishment of more opportunistic carabids and ensure the persistence of forest specialists, which provides the functional stability of forest ecosystems (Sitzia et al. 2017).

CONCLUSION

Our study demonstrated the existence of between-year variation in species richness, abundance, and diversity. This approach was more sensitive than functional traits to describe to between-year variation and structural changes of beetle assemblages in time. The functional traits approach revealed that treatment-induced differences were more important than between-year variation. We conclude that the simultaneous use of the two approaches will provide the most articulate understanding of the status of ground beetles assemblages in response to forest management. In addition, there is a functional potential in the studied ground beetles assemblages regardless of the variation in species composition and diversity in time and help to explore which group can be sensitive to disturbances. Moreover the functional redundancy in clear-cuts and retention-tree groups is related to the invasion of habitat generalist and open-habitat species with high dispersal power causing a decline in the population of true forest-dwelling carabids with weak dispersal ability. This functional difference remains consistent between years suggesting that the population of mostly carnivorous forest specialists with low dispersal power have not yet regenerated four years after implementation of the studied forestry treatments.

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SUPPORTING INFORMATION

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