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Species- and trait-based responses of carabids to rotation and closer-to-nature forestry in a temperate forest under changing climate

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Abstract

1. European temperate forests are managed by various silvicultural practices that can impact ground beetles (Coleoptera: Carabidae) in terms of species composition and abundance. However, the responses at the assemblage or community level may not provide sufficient insight into how individual species react to forest management.
2. We examined the species- and trait-based mid-term (2014–2018) responses of the eight most common carabid species in a managed oak-hornbeam forest in Hungary. The studied forestry treatments included preparation cutting, clear-cutting, green tree retention, gap cutting, and undisturbed control plots.
3. Species responses varied across forestry treatments and years, but clear-cutting consistently had a negative impact on multiple species, particularly on *Abax parallelepipedus*, *Aptinus bombarda*, and *Carabus hortensis*. In contrast, the abundance of *Carabus coriaceus* and *Carabus ullrichii* declined after an initial burst in the newly established treatments. Functional traits also influenced the responses; forest specialists and spring and autumn breeders were negatively affected by clear-cutting and retention, followed by an overall decline in their abundance. Notwithstanding, habitat generalists and species without a defined breeding season exhibited more stable abundance trends over the years.
4. These declines may be linked to phenological shifts driven by climate change. Spring breeders may have extended their activity period, leading to increased competition with autumn breeders in late summer and autumn when tenerals of spring breeders emerge. Although our study presents mid-term trends, we believe that it provides a further understanding of the responses of carabid species in managed temperate forests.

KEYWORDS
biotic homogenization, forest management, ground beetles, insect decline, phenological shifts, temperate forest

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INTRODUCTION

The majority of European forests are subject to a range of silvicultural practices that can significantly influence natural forest dynamics. Forest management can alter habitat structures, environmental conditions, microclimate, and resource availability (Bengtsson et al., 2000; Paillet et al., 2010; Schall et al., 2018). In the last two decades, there has been a growing interest throughout Europe in replacing traditional even-aged rotation forestry with new approaches. These alternatives integrate better economic and biodiversity conservation objectives (Mason et al., 2022; Pommerening & Murphy, 2004). They are often referred to as "closer-to-nature" silvicultural systems, which aim to mimic natural forest dynamics by maintaining uneven-aged stands with continuous canopy cover and minimising large-scale disturbances such as clear-cutting (Bengtsson et al., 2000; Pommerening & Murphy, 2004). The underlying assumption is that uneven-aged forestry promotes local biodiversity within forest stands by creating heterogeneity in microhabitats and niches (Pro Silva, 2012; Samu et al., 2023). Yet, rotational management remains more prevalent in Europe, with only 30% of temperate forests managed using the closer-to-nature approach (Aszalós et al., 2022; Mason et al., 2022). The resilience of managed forests, regardless of implemented forestry practices, and forest biodiversity will face additional challenges and uncertainties due to climate change (Cours et al., 2023; O'Hara, 2016).

As climate change progresses and interacts with local management practices, it significantly alters forest habitats, environmental conditions, and resource availability. These changes directly impact and filter forest insect communities, affecting their composition, spatial and temporal distribution, and taxonomic and functional diversity (Dörfler et al., 2018; Schall et al., 2018; Staab et al., 2023; Wagner et al., 2021). It can also lead to biotic homogenization by selecting only certain species or traits (McKinney & Lockwood, 1999). Additionally, as ectotherms, insects are highly sensitive to these changes and can respond in their phenology — the seasonal timing of biological processes (Boggs, 2016). This sensitivity can lead to mismatches in seasonal activity patterns, thereby altering trophic relationships in managed forests (Forrest, 2016; Schleuning et al., 2020; Staab et al., 2023; Van Dyck et al., 2015). Although it can be argued that some trophic guilds, such as pollinators or phytophagous species, may be more susceptible than predators (Jactel et al., 2019; Murray et al., 2017), the forest food network is tightly connected and affected as a whole (Cours et al., 2023). Thus, understanding trends in insect populations and communities with functional roles like predation and pest control is essential too and should not be overlooked (Staab & Schuldt, 2020).

Carabid beetles (Coleoptera: Carabidae) are a diverse and ecologically important group of insects found in terrestrial ecosystems, including forests. As adults, they are mostly predators positioned in the middle of the trophic cascade and often serve as bioindicators and early warning signalers for environmental and climatic change (Brooks et al., 2012; Homburg et al., 2019; Lövei & Sunderland, 1996). Climate change has been observed to significantly affect the distribution of carabid species along altitudinal gradients in mountainous regions, resulting in an uphill shift of previously lowland species or even local extinction (Brandmayr & Pizzolotto, 2016; Chamberlain et al., 2020). In European managed forests, carabids have been found to sensitively react to various forestry treatments, leading to changes in their species composition and abundances (e.g., Heikkala et al., 2016; Koivula et al., 2019; Lange et al., 2014; Negro et al., 2014). A functional trait-based assessment is increasingly being discussed as a potential mechanism underlying the community structure of forest carabids (Homburg et al., 2019; Nolte et al., 2017; Weiss, Winter, et al., 2024). Previously, we found that carabid communities in forested areas managed by rotational forestry appeared to be functionally redundant, suggesting that multiple species perform similar roles in the forest ecosystem, compensating for any loss from the species pool (Elek et al., 2022). Yet, it is still not widely studied how individual carabid species respond in terms of abundance to the implemented forest management. Some of their functional traits that are related to their life history, such as overwintering and breeding, could well reflect habitat quality and use (Henle et al., 2004). Interestingly, phenological aspects in carabids remain poorly studied (Homburg et al., 2019). Furthermore, due to the close connection between taxonomic identity and functional traits in this monophyletic group (Magura & Lövei, 2019; Negro et al., 2014), species-specific responses can complement the functional approach to understand variations in species and traits across different forestry treatments. This perspective also allows us to identify species that are most vulnerable to habitat alterations or most critical for ecosystem functioning.

In this study, we aimed to explore in detail the mid-term impact of different forestry treatments in Hungarian oak-hornbeam forests on species- and trait-specific responses of carabids. Previously, we found that over time, the overall species richness and activity-density decreased in all studied forestry treatments with a short immediate mass effect in freshly managed plots (Elek et al., 2022). Such an overall decline prompted us to conduct a detailed analysis of the mid-term responses of the most dominant species (to ensure the representativeness of the data). We also considered selected functional traits that are directly linked to the development and habitat affinity. Two different silvicultural systems represented our focal forestry treatments. First, traditional rotation forestry was characterised by preparation cuttings and clear-cuttings with green tree retentions. Second, closer-to-nature forestry mimicked natural forest disturbances in the form of small-scale gaps in the canopy. As closer-to-nature forestry involves the maintenance of permanent forest canopy cover, it can be hypothesised that this approach continuously keeps characteristics of an uneven-aged natural forest and offers better performance in maintaining ecosystem services, conserving biodiversity, including carabids, and mitigating the impact of climate change better than rotation forestry (Bengtsson et al., 2000; Pommerening & Murphy, 2004).

Specifically, we explored (1) the mid-term (5 years) changes in the abundances of the most dominant carabid species and (2) the changes in the species composition and trait variation between treatments and years. We hypothesised that the abundance of particular species will change more substantially in clear-cuttings than in other treatments

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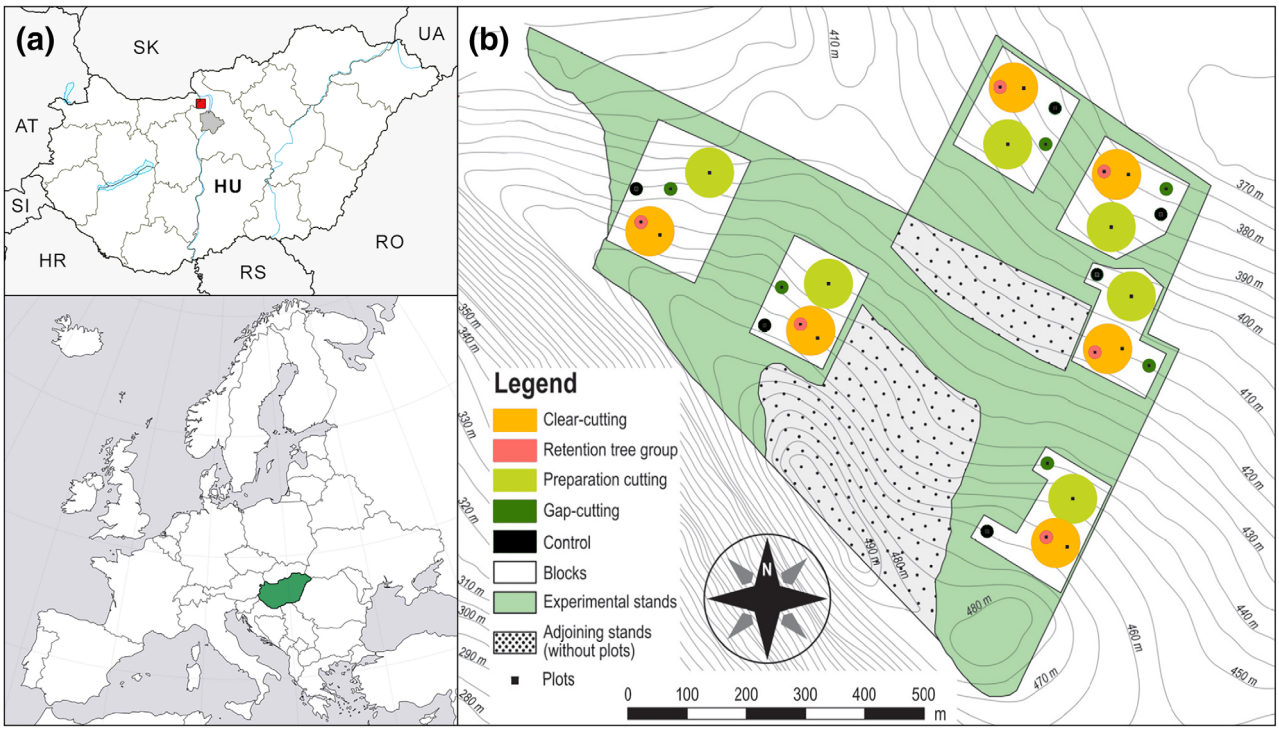

FIGURE 1 (a) Location of the study area in the Pilis Mountains in northern Hungary (red square) and (b) the overview of the Pilis Forestry Systems Experiment's design. Countries are AT, Austria; HU, Hungary; HR, Croatia; RO, Romania; RS, Serbia; SK, Slovakia; SI, Slovenia; UA, Ukraine.

due to increased canopy openness. Additionally, we expect that at least some forest specialists will decline in response to the implementation of forestry treatments, while habitat generalists will either remain stable or increase over time.

MATERIALS AND METHODS

Study area and experimental design

The study area is situated within the Pilis Mountains of northern Hungary (47.674° N, 18.908° E, Figure 1a), and it is a part of the Pilis Forestry Systems Experiment (project website: https://piliskiserlet.ecolres.hu/en). The elevation ranges from approximately 370 to 470 meters above sea level, with an annual precipitation between 600 and 650 mm and an average temperature ranging from 9.0°C to 9.5°C (Dövényi, 2010). The experimental area encompasses approximately 40 hectares and hosts an 80-year-old oak-hornbeam forest (Natura 2000 code: 91G0, European Commission, 1992). Originally, this forest was managed using a shelterwood silvicultural system, resulting in a two-layered canopy stand. The upper canopy layer was predominantly composed of sessile oak (*Quercus petraea* (Matt.) Liebl.), with an average height of 21 m and a diameter at breast height of 28 cm. The secondary canopy layer primarily consisted of hornbeam (*Carpinus betulus* L.), with an average height of 11 m and a mean diameter of 12 cm. Other admixture tree species included *Quercus cerris* L., 1753, *Fagus sylvatica* L., 1753, *Prunus avium* L., 1753, and *Fraxinus ornus* L., 1753. The shrub layer was sparse, mostly with regeneration of hornbeam and manna ash. The understory vegetation was dominated by mesic forest plants, such as *Carex pilosa* Scopoli, 1772, and *Melica uniflora* Retz, 1779.

Established in 2014, the Pilis Forestry Systems Experiment aims to compare two different silvicultural systems: regionally dominant rotation forestry and closer-to-nature forestry, and assess their effects on the forest stand (Kovács et al., 2020), biodiversity (Boros et al., 2019; Elek et al., 2018, 2022; Samu et al., 2021), and regeneration (Tinya et al., 2020). The rotation forestry system was characterised by preparation cuttings, clear-cuttings, and green tree retentions, while the most widely used treatment from the closer-to-nature forestry was represented by small-scale canopy gaps. Additionally, there were undisturbed control plots without any treatment. The study design followed a complete block design, employing six blocks as replicates (see Figure 1b), resulting in a total of 30 plots that were considered as basic sampling units. Treatments and their replicates were established in winter 2014/2015 by Pilisi Parkerdő Ltd. as follows:

1. In preparation cuttings (P), approximately 30% of the upper canopy layer and the whole secondary canopy layer were removed in a circular area of 0.5 ha (80 m diameter)
2. In clear-cuttings (CC), all trees were removed in a circular area of 0.5 ha (80 m diameter)
3. Green tree retentions (R) were created in the clear-cutting areas by keeping 8–12 dominant trees and all trees in a secondary canopy layer, resulting in a circular area with approximately 20 m in diameter.

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TABLE 1 Summary table of the species included in the analyses, showing their abundances (N) and functional traits related to habitat affinity and phenology.

Species	*N*	Habitat affinity	Overwintering	Breeding season
Abax parallelepipedus Piller & Mitterpacher, 1783	4496	Forest	Adult	Whole Season
Aptinus bombarda (Illiger, 1800)	1806	Forest	Adult	Spring
Carabus coriaceus L., 1758	1156	Forest	Larva And Adult	Autumn
Carabus hortensis L., 1758	4869	Forest	Larva And Adult	Autumn
Carabus scheidleri Panzer, 1799	3082	Generalist	Larva And Adult	Whole Season
Carabus ullrichii Germar, 1824	1442	Forest	Adult	Spring
Nebria brevicollis (F., 1792)	1044	Generalist	Larva And Adult	Autumn
Pterostichus melanarius (Illiger, 1798)	786	Generalist	Larva And Adult	Whole Season

Note: Trait data were obtained from Thiele (1977); Lindroth (1985; 1986); Hůrka (1996), and Turin et al. (2003).

4. Gaps (G) were created in the closed forest as a circular, small canopy gap with a diameter of 20 m.
5. Controls (C) were undisturbed closed forests

Carabid sampling

Data collection adhered to the Before-After Control-Impact (BACI) concept, as proposed by Green (1979). Initially, we sampled all plots before the implementation of forestry treatments in 2014, using these pre-treatment data as a baseline. Subsequently, we conducted data collection over the following four years, from 2015 to 2018. In each plot (see Figure 1b), we installed four pitfall traps in the nodes of a 5-m grid to sample carabids, resulting in a total of 120 traps per sampling session. Traps were open for one month during the spring (June) and autumn (September), covering the activity peak of carabids. The pitfall traps were constructed using plastic cups with an 85 mm diameter, filled with approximately 250 cm^3 of a 50% solution of propylene glycol and water, which was saturated with salt and a drop of odourless detergent to reduce surface tension. Dark green plastic roofs were installed to protect traps from rainfall and litter. For carabid determination, we used the keys of Hůrka (1996); Lindroth (1985; 1986) and followed the taxonomy established by Hůrka (1996).

Data analyses

Carabid abundance data from each plot (i.e., four pitfall traps) per year were pooled and considered as a basic unit for further analyses. To ensure data robustness and the model estimates, we selected those species present in all treatments with at least 700 individuals as total abundance between 2014 and 2018. For each of the eight selected species, we collected traits related to their life history and ecology, as these traits might act as signs of habitat alteration and climate change (Forrest, 2016; Henle et al., 2004; Nolte et al., 2019). In particular, we categorised these species according to their habitat affinity (forest-habitat specialists and generalist species), overwintering stage (adult, larva and adult), and breeding season (spring breeders, autumn breeders, and breeding unrelated to season). These traits were obtained from Thiele (1977); Lindroth (1985; 1986), Hůrka (1996), and Turin et al. (2003). The complete list of selected species, including their abundances and traits, is provided in Table 1.

The species- and trait-specific, as well as total abundance responses, to forestry treatments and years were evaluated by zero-inflated generalised linear mixed models using the *glmmTMB* function from the 'glmmTMB' package (Brooks et al., 2017). As explanatory variables, the models included treatment (a factor with five levels, with "control" as the reference), year (a factor with five levels, with "2014" as the baseline), and their interaction as fixed effects to account for year-specific seasonal variation in responses between treatments. The block (a factor with six levels) was included as a random intercept to account for spatial variation between replicates. The model included a single zero-inflation parameter applying to all observations ($zi = \sim 1$), except the total abundance, where zero-inflation was not used. To determine the most appropriate distribution for each response, we compared models with three different distributions: negative binomial (linear and quadratic) and generalised Poisson, as they can be suitable for overdispersed count data (Yadav et al., 2021). Model selection was based on the comparison of the Akaike Information Criterion using the *model.sel* function in the 'MuMIn' package (Bartoń, 2024), where the $\Delta AIC = 2$. The results of model selection are presented in supplementary Tables A1 and A2. After selecting the best-fitting model, we assessed model fit by simulating residuals with the *simulateResiduals* function from the 'DHARMa' package (Hartig et al., 2024) to check for potential violations of model assumptions. For testing the dependence of response variables on the selected explanatory factorial ones with reference groups (i.e., significance of fixed effects), we performed an ANOVA with type III estimates for the sum of squares using the 'car' package (Fox & Weisberg, 2018). To control for the increased risk of Type I errors due to multiple testing, we adjusted p-values from the best models using Hochberg's correction, which is appropriate under the assumption of independent or positively correlated tests (Hochberg, 1988). The adjusted *p*-values were computed using the *p.adjust* function from the 'stats' package (version 3.6.2) with the method set to

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TABLE 2 Summary of the best generalised mixed models for species-specific responses to forestry treatments, year, and their interaction.

Species	Distribution	Explanatory variable	χ^2	df	*p*
Abax parallelepipedus	nbinom2	**Intercept**	**228.586**	**1**	**<0.001**
		Treatment	2.084	4	0.720
		Year	**99.576**	**4**	**<0.001**
		Treatment × Year	**68.037**	**16**	**<0.001**
Aptinus bombarda	nbinom2	**Intercept**	**139.622**	**1**	**<0.001**
		Treatment	2.033	4	0.730
		Year	**81.402**	**4**	**<0.001**
		Treatment × Year	**44.767**	**16**	**<0.001**
Carabus coriaceus	nbinom2	**Intercept**	**5.638**	**1**	**0.035**
		Treatment	2.820	4	0.588
		Year	**102.798**	**4**	**<0.001**
		Treatment × Year	**38.445**	**16**	**0.004**
Carabus hortensis	nbinom2	**Intercept**	**151.766**	**1**	**<0.001**
		Treatment	6.397	4	0.171
		Year	**206.354**	**4**	**<0.001**
		Treatment × Year	**57.737**	**16**	**<0.001**
Carabus scheidleri	genpois	**Intercept**	**51.144**	**1**	**<0.001**
		Treatment	5.909	4	0.206
		Year	**17.577**	**4**	**0.004**
		Treatment × Year	**30.859**	**16**	**0.028**
Carabus ullrichii	nbinom2	Intercept	3.489	1	0.185
		Treatment	3.590	4	0.464
		Year	**40.817**	**4**	**<0.001**
		Treatment × Year	16.373	16	0.464
Nebria brevicollis	genpois	Intercept	1.031	1	0.620
		Treatment	1.958	4	0.743
		Year	**13.865**	**4**	**0.031**
		Treatment × Year	22.400	16	0.392
Pterostichus melanarius	nbinom2	**Intercept**	**10.212**	**1**	**0.004**
		Treatment	3.254	4	0.516
		Year	**15.671**	**4**	**0.007**
		Treatment × Year	**43.222**	**16**	**0.001**

Note: Species abundance data were modelled using either a negative binomial quadratic (nbinom2) or generalised Poisson (genpois) distribution. Significant effects are highlighted in bold, and *p*-values were adjusted for multiple testing using Hochberg's correction.

"hochberg" (R Core Team, 2023). Model-predicted means (estimated marginal means) for each treatment and year combination were obtained using the *emmeans* function from the 'emmeans' package (Lenth, 2025).

Non-metric multidimensional scaling (NMDS) was applied to test dissimilarities in the composition of carabid species across forestry treatments and years based on the Bray–Curtis similarity matrix for abundance data with the Hellinger transformation, using the *metaMDS* function from the 'vegan' package (Oksanen, 2025). Differences in species composition were tested using Permutational Multivariate Analysis of Variance (PERMANOVA) by the *adonis2* function from the 'vegan' package. The model included treatment, year, and their interaction as explanatory variables, with 10,000 permutations to assess significance. All analyses with the use of the modular packages have been implemented in R 4.3.2 (R Core Team, 2023).

RESULTS

In total, 18,681 individuals of eight carabid species were included in the analyses. *Carabus hortensis* L., 1758 (4869 individuals), *Abax parallelepipedus* Piller & Mitterpacher, 1783 (4496 ind.), and *Carabus scheidleri* Panzer, 1799 (3082 ind.) were the most abundant species (Table 1). Species-specific responses were influenced by both forestry

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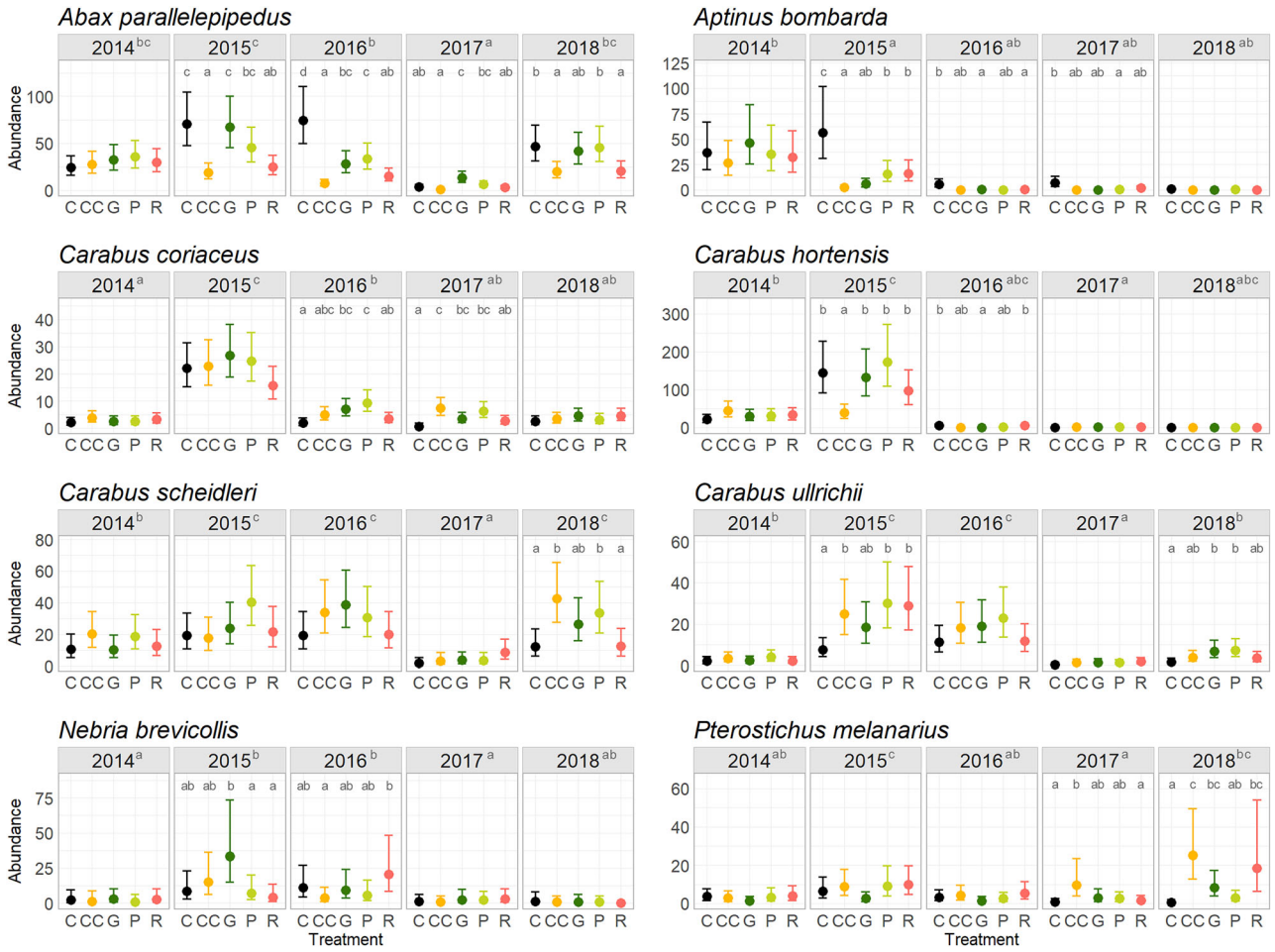

FIGURE 2 Estimated marginal means for species abundances across different treatments and years. The solid dots represent predicted means, and vertical lines indicate 95% confidence intervals. Different lowercase letters denote significant differences among treatments and years, based on Tukey's multiple comparisons of means. The abbreviations of forestry treatments are controls (C), clear-cuttings (CC), gaps (G), preparation cuttings (P), and retentions (R).

treatments and inter-annual variation (see Table 2 for model outputs), with each species exhibiting a distinct pattern (Figure 2, also see Figure SA1 for raw abundances). *A. parallelepipedus* showed moderate fluctuations between years, with the most consistent response to forestry treatments, significantly declining in clear-cuttings (CC) and green tree retentions (R) compared to undisturbed controls (C). It also had a varying response to gaps (G). *Aptinus bombarda* Piller & Mitterpacher, 1783 had a negative response to all treatments in most years and gradually disappeared from the study area. Among large carabids, the abundance of *Carabus coriaceus* L., 1758 peaked in the first year following treatment implementation, after which it was more frequently recorded in CC, preparation cuttings (P), and G compared to control plots. In contrast, *C. hortensis* exhibited an immediate negative response to fresh clear-cuttings and, from 2016 onward, nearly disappeared from all treatments as well as controls. *C. scheidleri* remained relatively stable in numbers across all forestry treatments, with a slight preference for CC and P (especially in 2018), and only minor between-year fluctuations. The abundance of *Carabus ullrichii* Germar, 1824 showed an initial burst in newly implemented treatments in 2015 and 2016, particularly in CC, P, and R, and this trend remained similar, although not as pronounced, and with varying responses to G in the following years. In contrast, *Nebria brevicollis* (F., 1792) showed erratic peaks, reaching its highest abundance in gaps in 2015 and in retentions in 2016, while remaining low elsewhere, while *Pterostichus melanarius* (Illiger, 1798) responded positively to CC and, in 2018, also to R and G.

Considering functional traits (Table 3, Figure 3, for raw abundances, see Figure A2), CC and later years also R had a negative impact on forest species, leading to an overall decline in their abundance. In contrast, habitat generalists exhibited the opposite trend, increasing in CC and R while maintaining a more stable temporal pattern in abundance. Species that overwinter as adults were generally more abundant in control plots, showing a negative response to CC and R. Species that overwinter in both adult and larval stages had an inconsistent, fluctuating response, with a negative response to controls and gradually declined toward 2018. Species without a defined breeding season were initially negatively affected by the newly implemented CC and R treatments. However, as succession progressed,

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TABLE 3 Summary of the best generalised mixed models for trait-based responses and all individuals to forestry treatments, year, and their interaction.

Functional trait	Distribution	Explanatory variable	χ^2	df	*p*
Habitat: Forest species	nbinom2	**Intercept**	**881.728**	**1**	**<0.001**
		Treatment	0.835	4	0.934
		Year	**192.996**	**4**	**<0.001**
		Treatment × Year	**39.994**	**16**	**0.002**
Habitat: Generalist species	genpois	**Intercept**	**98.705**	**1**	**<0.001**
		Treatment	5.028	4	0.284
		Year	**30.023**	**4**	**<0.001**
		Treatment × Year	**39.585**	**16**	**0.002**
Overwintering: Adult	genpois	**Intercept**	**614.099**	**1**	**<0.001**
		Treatment	2.642	4	0.619
		Year	**65.867**	**4**	**<0.001**
		Treatment × Year	24.391	16	0.163
Overwintering: Larva and adult	nbinom2	**Intercept**	**375.452**	**1**	**<0.001**
		Treatment	7.114	4	0.130
		Year	**180.935**	**4**	**<0.001**
		Treatment × Year	**64.010**	**16**	**<0.001**
Breeding: Whole season	genpois	**Intercept**	**250.476**	**1**	**<0.001**
		Treatment	3.620	4	0.460
		Year	**62.095**	**4**	**<0.001**
		Treatment × Year	**36.778**	**16**	**0.005**
Breeding: Spring	nbinom2	**Intercept**	**229.393**	**1**	**<0.001**
		Treatment	1.472	4	0.832
		Year	**80.776**	**4**	**<0.001**
		Treatment × Year	**39.559**	**16**	**0.002**
Breeding: Autumn	genpois	**Intercept**	**203.220**	**1**	**<0.001**
		Treatment	7.176	4	0.127
		Year	**164.922**	4	**<0.001**
		Treatment × Year	**51.834**	16	**<0.001**
All individuals	genpois	**Intercept**	**1040.578**	**1**	**<0.001**
		Treatment	2.578	4	0.631
		Year	**184.025**	**4**	**<0.001**
		Treatment × Year	**46.741**	**16**	**<0.001**

Note: Abundance data were modelled using either a negative binomial quadratic (nbinom2) or generalised Poisson (genpois) distribution. Significant effects are highlighted in bold, and *p*-values were adjusted for multiple testing using Hochberg's correction.

this effect diminished, resulting in only minor abundance fluctuations across years. In contrast, both spring and autumn breeders responded negatively to CC, and some years also to R and G, with a gradual disappearance from the study area. In addition, the forest species, species overwintering as larva and adult, and autumn breeders show an initial burst in their abundance in 2015 due to the foundation effect of forestry treatments in 2014. Finally, the total abundance of the studied species followed a similar trend as previously described, showing a negative response to newly implemented CC and R treatments, peaking in 2015, and gradually declining toward 2018 with a diminishing negative effect of CC.

Following NMDS biplots, we observed an effect of forestry treatment and between-year variation on the composition of the most abundant species (Figure 4); gradually diverging after treatment implementation in 2015. Especially clear-cuttings, and to some extent also green tree retentions, clearly differ from controls. This pattern was supported by PERMANOVA results showing a significant effect of treatment ($R^2 = 0.100$, $F = 7.392$, $p < 0.001$), year ($R^2 = 0.387$, $F = 28.670$, $p < 0.001$), and their interaction ($R^2 = 0.091$, $F = 1.675$, $p = 0.003$), suggesting that changes in species composition were affected by both temporal dynamics and forestry treatment type.

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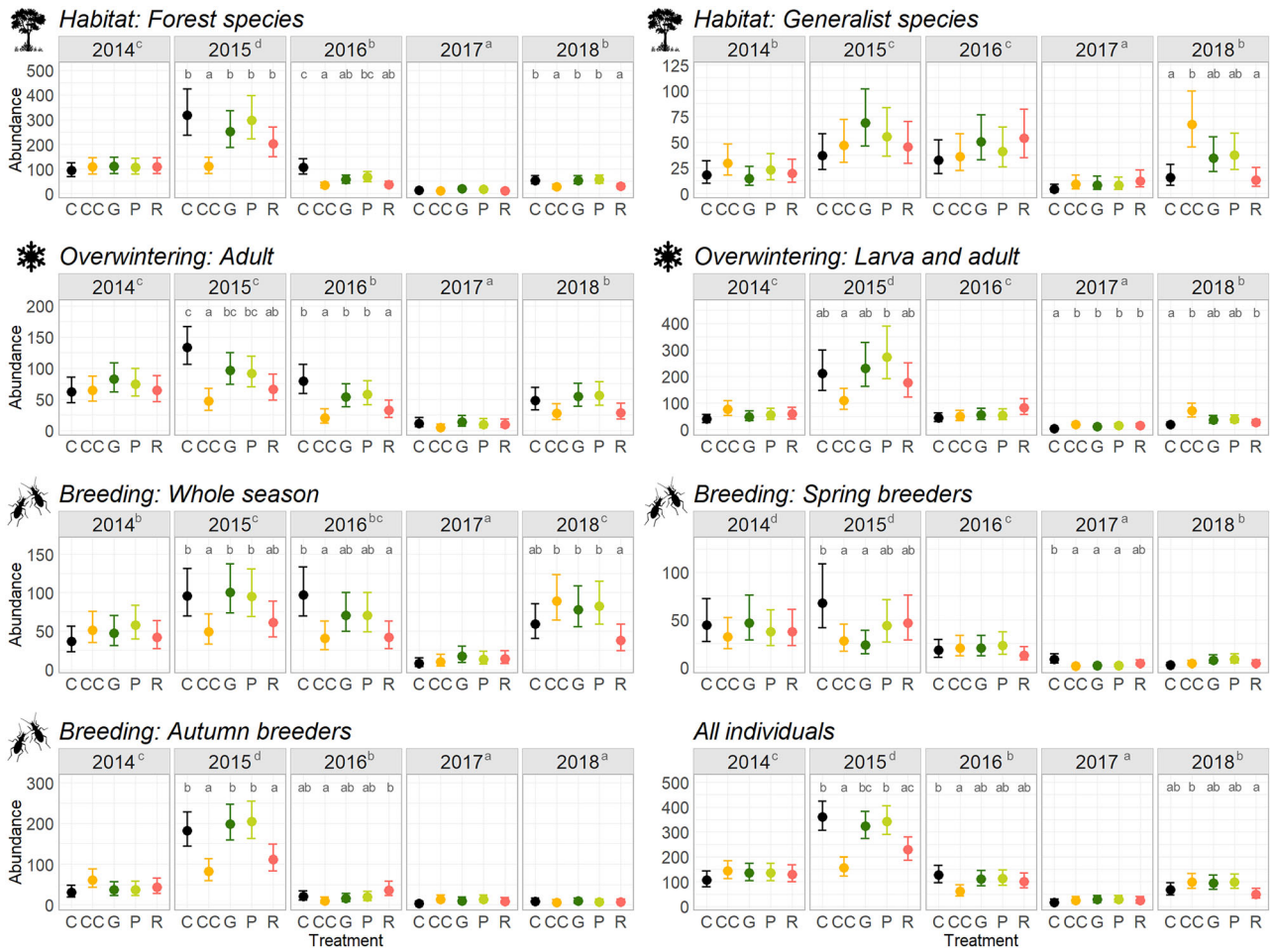

FIGURE 3 Estimated marginal means for trait-specific abundances and total abundance across different treatments and years. The solid dots represent predicted means, and vertical lines indicate 95% confidence intervals. Different lowercase letters denote significant differences among treatments and years, based on Tukey's multiple comparisons of means. The abbreviations of forestry treatments are controls (C), clear-cuttings (CC), gaps (G), preparation cuttings (P), and retentions (R).

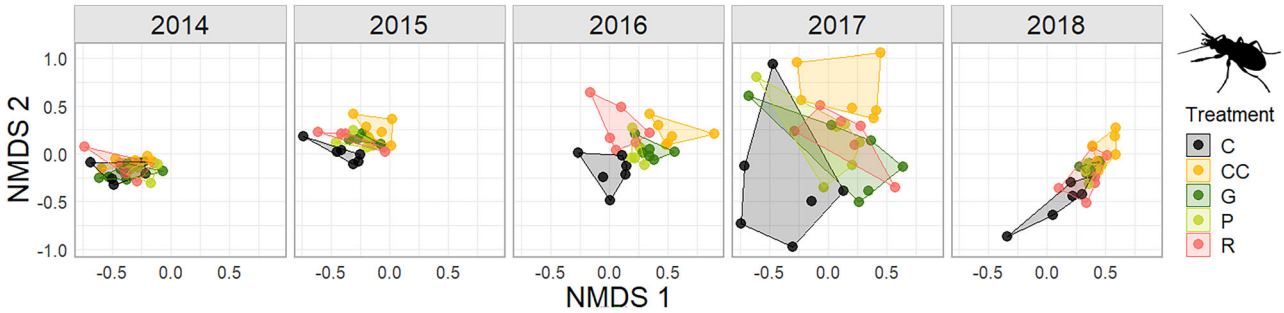

FIGURE 4 Non-metric multidimensional scaling (NMDS) biplots of eight carabid species captured across different forestry treatments and years using the Bray–Curtis dissimilarity matrix (overall stress value = 0.190). Points represent individual plots, and convex hulls delineate the treatment groups within each year to illustrate temporal changes. The abbreviations of forestry treatments are controls (C), clear-cuttings (CC), gaps (G), preparation cuttings (P), and retentions (R).

DISCUSSION

In our study, we observed two levels of carabid responses: first, responses linked to the specific forestry treatment, and second, broader temporal responses that were rather independent of the treatment, which occurred consistently across the whole study site, including control plots. Although some of the focal species shared a specific set of traits, they did not respond in the same way to the

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implemented treatments. Some carabid species always responded negatively, while others remained unchanged, highlighting that species-specific responses can complement assemblage-level studies (Elek et al., 2022). Focusing on forestry treatments, clear cuttings, and, to some extent, also green tree retentions had the most significant impact on species-specific abundance and trait composition of the assemblage, which supports our first hypothesis. This predominantly negative effect, especially in the first year after implementation, could possibly be caused by changes in microclimate due to increased canopy openness. If we look beyond the treatment scale, we find very similar declining responses of some traits in the whole study system, including undisturbed forests. Following our second hypothesis, only habitat generalists and species without specific breeding seasons showed relatively stable abundances across all study years, while others mostly decreased. These findings suggest a possibility of biotic homogenization and/or phenological shift of certain species and their traits because carabids could either completely disappear or shift their activity to different times out of our sampling sessions. Interestingly, the overall decrease in abundance was not observed in other previously studied groups in the area, including ground-dwelling spiders or soil organisms (Boros et al., 2019; Samu et al., 2021), suggesting higher sensitivity of (at least some) carabids to changes in forest habitat. Although the Pilis Forestry Systems Experiment was designed to reduce the edge effect on the examined forest biota, we cannot fully exclude its influence on relatively mobile carabids. As the recent study by Magura and Lövei (2024) showed, the depth of edge influence can extend up to 300 m into forest stands if edges are created by various forestry operations. The shortest distance between different forestry treatments, thus, should exceed 600 m to fully avoid the edge effect.

Studies focusing on carabids often assess their responses to various silvicultural practices at the sub-assemblage or community level (e.g., Heikkala et al., 2016; Koivula et al., 2019; Negro et al., 2014). Their relevance is indisputable; however, overall changes in species richness, activity-density, or functional diversity of the assemblage cannot provide details about the responses of a particular species (e.g., Koivula et al., 2002). For instance, is there any species more vulnerable than the other? The species in this study often shared the same set of traits formed by carnivorous, brachypterous forest specialists that frequently occur in sessile oak-hornbeam forests of Hungary (Elek et al., 2022). It is quite evident that some forest-associated species were negatively affected by newly implemented clear-cuttings due to higher temperatures, lower humidity, and greater daily fluctuations in microclimatic conditions compared to undisturbed forests (Kovács et al., 2020). However, the rapid development of shrubs and tree seedlings following logging (Tinya et al., 2020) may mitigate extreme microclimatic conditions at ground level by providing thermal refugia, thereby reducing the initial negative impact of clear-cuttings as succession progresses. Notably, *P. melanarius*, a generalist species, showed an increase in abundance under these altered conditions, particularly in the later stages of the study. In addition, the abundance of some larger forest-associated species, such as *C. coriaceus* and *C. ullrichii*, initially increased in the new treatments, including clear-cuttings. These species likely used forestry treatments and their edges for foraging or mating to avoid competition with other large carabids in the closed forest (Růžičková et al., 2021; Růžičková & Veselý, 2018). As proposed by Lindenmayer et al. (2012), keeping a group of retention trees in large clear-cutting areas can help support forest biodiversity by maintaining forest structure. Retentions may delay some responses; however, due to their relatively small size (20 m diameter), they can function similarly to clear-cuttings rather than large-sized retentions (Lindenmayer et al., 2012; Yamanaka et al., 2021) and do not enhance species or functional richness in harvested forests (Sultaire et al., 2021). Preparation cuttings did not affect responses to such an extent as open clear-cuttings. Partial canopy openness is still able to keep a relatively humid forest environment, and the development of understory vegetation can have a buffering effect by promoting structural and microhabitat heterogeneity (Kovács et al., 2020; Negro et al., 2014), which can support the persistence of forest carabids (Sitzia et al., 2015). Small-scale canopy gaps are intended to mimic natural forest dynamics and may help mitigate forest changes (Pommerening & Murphy, 2004). In our study, species- and trait-based responses were generally similar to those in control plots, supporting the primary objective of continuous cover forestry, with a few instances of relatively random abundance peaks, such as *N. brevicollis* in 2015. Contrarily, two species typical for closed temperate forests (Magura et al., 2003), *A. bombarda* and *C. hortensis*, were very sensitive not only to silvicultural interventions but also to overall temporal changes in forest stands, as they gradually declined in all treatments as well as undisturbed controls. Similarly, Weiss, von Wehrden, and Linde (2024) also identified *C. hortensis* as one of the most declining carabid species in a temperate forest in Germany. In contrast, other species of similar size, such as *C. coriaceus* and *C. ullrichii*, did not exhibit as pronounced a decline across the study area. So, even sharing a very similar set of traits related to habitat preferences, there are winners and losers regardless of used forest management.

Species in this study exhibited variations in their overwintering stage and breeding season, thus traits linked to development and higher sensitivity to climatic changes (Henle et al., 2004; Homburg et al., 2019). Carabids typically have one reproductive cycle per year, breeding either in spring or autumn (Thiele, 1977). Our results indicate that species without a defined breeding season showed only minor fluctuations over time, while spring and autumn breeders were more negatively affected, with a gradual decline. Given these trait-specific responses, it is likely that breeding phenology plays a key role in shaping species' reactions to forestry treatments, potentially interacting with climatic factors rather than being solely determined by local stand structure. These findings seem to be partially opposite to the previous findings that reported a greater decline among spring breeders compared to autumn breeders in European forests (Homburg et al., 2019) because larval instars are the most sensitive stages of carabid development and can not cope well with thermal stress (Lövei & Sunderland, 1996). Moreover, some of the autumn breeders live more than one year, so the population has different age classes, allowing a better tolerance in adverse climatic conditions

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(Baumgartner et al., 1997). We may suggest that some phenological shifts likely occurred in our study system that could be responsible for the change in the activity peak and breeding season of some species. Although we are aware of the limitations to fully explain the long-term population trends of the studied carabid species, which is given by the relative brevity of our five-year study for such conclusions (Didham et al., 2020; Fournier et al., 2019; White, 2019), we want to point out some signs that could lead to phenological shifts.

In general, phenological shifts have already been observed in many insects with various levels and directions. For instance, some species can react with faster development and thus have more generations per season (Buckley, 2022; Harvey et al., 2023). However, the extended period of warmer temperatures may also result in a so-called developmental trap when a generation at the end of the season can not survive or enter winter diapause (the so-called lost generation hypothesis; see Van Dyck et al., 2015). The high variation in the length of mild winters may delay the spring emergence of other species due to the requirement of freezing periods during overwintering, or they do not emerge at all (Bale & Hayward, 2010). Species with early seasonal activity that frequently overwinter as adults can shift their activity and breeding even earlier in the season (Forrest, 2016; Irmler, 2022). This activity shift could be our case because spring breeding carabids declined in pitfall trap catches. As the suitable period for breeding likely moved earlier in spring, out of our spring sampling period (June), larval instars could avoid drought stress during the warm summer (Homburg et al., 2019). Then, however, tenerals of spring breeders emerged at the same time when autumn breeders became active, which caused an overlap in activity. Since autumn breeders need more resources due to the reproduction period than spring breeders, that "only" look for enough food intake to survive overwintering, this competition may lead to the decline of adult autumn breeders. Moreover, not only the larvae but also a considerable proportion of adults of autumn breeders hibernate, after which they can enter a second reproductive period (Lövei & Sunderland, 1996) that requires even more resources. In this competition game, species with a flexible reproductive period, e.g., *A. parallelepipedus* and *C. scheidleri*, can escape temperature extremes and precipitation deficits to more suitable parts of the year, assuring the persistence of species populations (Andorkó & Kádár, 2009; Thiele, 1977). Given that these species seem to be unaffected, in parallel with phenological shifts, our findings can also be explained by biotic homogenization (Jung et al., 2018; Marrec et al., 2021; McKinney & Lockwood, 1999). Changes in the forest, either at or beyond the treatment level, may act as an environmental filter that supports only generalist species without specific habitat requirements and flexible breeding, while (some) more sensitive forest specialists decline in numbers.

Besides the above-mentioned limitations, it can also be argued that our baseline year 2014 could be atypical in terms of climatic conditions (e.g., warmer and/or drier than usual), leading to lower numbers of mostly forest-associated species in yet-unmanaged forest sites. However, in such a scenario, we could not observe any decreasing trends in their abundances but rather neutral or even positive responses during the years in controls. Although the overall generalisation of our findings obtained only from a single site is limited (as also suggested by Lange et al. (2014) and Fournier et al. (2019), our study could be considered a case of phenological mismatches and biotic homogenisation in insect forest communities, possibly leading to decreasing insect biodiversity across forest ecosystems due to competitive exclusion.

CONCLUSIONS

Forest canopy can partially buffer climatic changes and potentially lower the extinction risk for carabid beetles compared to more open habitats (Brooks et al., 2012; Kotze & O'hara, 2003; Nolte et al., 2019); still, there are winners and losers among carabid species within forest ecosystems even when they are sharing similar functional traits. Our findings highlight the importance of combining the species- and trait-specific responses when assessing the ecological consequences of various forestry practices in temperate forests. Being aware of the relative intermediate timescale of our study for the assessment of long-term population trends, we emphasise the need for further research on the longstanding changes of carabid and other insect communities within managed forests under a changing climate, with special attention to phenological shifts and biotic homogenization. The potential impact of changes in seasonal activity on the network structure of insect communities remains inadequately understood. Such knowledge is vital for developing effective conservation strategies and sustainable management approaches.

AUTHOR CONTRIBUTIONS

Jana Růžičková: Investigation; formal analysis; data curation; writing – original draft; visualization. **Péter Ódor:** Funding acquisition; conceptualization; methodology; writing – review and editing. **Tibor Magura:** Writing – review and editing. **Zoltán Elek:** Conceptualization; methodology; investigation; formal analysis; writing – original draft; data curation.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository at: https://doi.org/10.5061/dryad.wdbrv15zv.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Species-specific model selection summary comparing different data distributions (negative binomial linear [nbinom1], negative binomial quadratic [nbinom2], and generalized Poisson [genpois]) based on AICc values. The AICc values are used to calculate the weight of evidence in favor of each model, with the most parsimonious model highlighted in bold.

Table S2. Trait-based model selection summary comparing different data distributions (negative binomial linear [nbinom1], negative binomial quadratic [nbinom2], and generalized Poisson [genpois]) based on AICc values. The AICc values are used to calculate the weight of evidence in favor of each model, with the most parsimonious model highlighted in bold.

Figure S1. Response of eight carabid species in terms of raw abundance to forestry treatments and years. Solid dots represent the mean and vertical lines indicate the 95% confidence interval. Different lowercase letters denote significant differences among treatments and years, based on Tukey's multiple comparisons of means. The abbreviations of forestry treatments are controls (C), clear-cuttings (CC), gaps (G), preparation cuttings (P) and retentions (R).

Figure S2. Response of seven categories of functional traits and total abundance to forestry treatments and years based on raw data. Solid dots represent the mean and vertical lines indicate the 95% confidence interval. Different lowercase letters denote significant differences among treatments and years, based on Tukey's multiple comparisons of means. The abbreviations of forestry treatments are controls (C), clear-cuttings (CC), gaps (G), preparation cuttings (P) and retentions (R).

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