

ORIGINAL ARTICLE

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 teneral 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

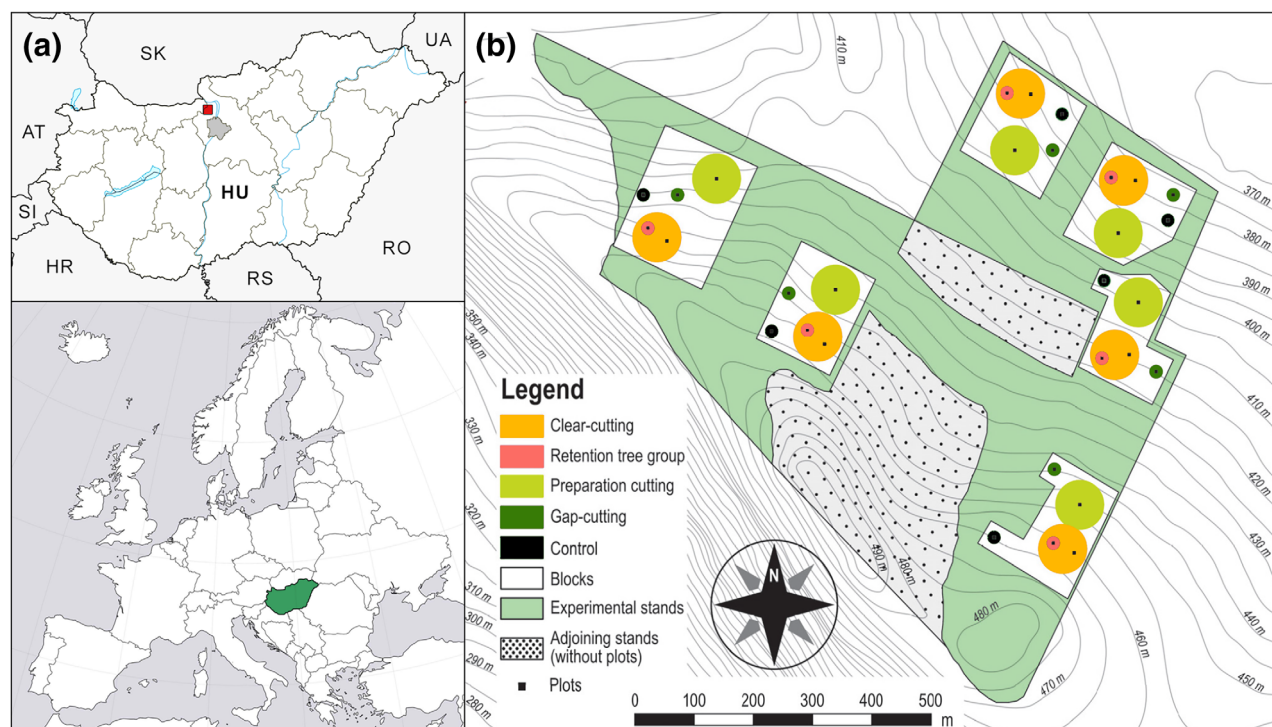


FIGURE 1 (a) Location of the study area in the Pilis Mountains in northern Hungary (red square) and (b) the overview of the Pilis Forestry Systems Experiment's design. Countries are AT, Austria; HU, Hungary; HR, Croatia; RO, Romania; RS, Serbia; SK, Slovakia; SI, Slovenia; UA, Ukraine.

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.

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

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

- Gaps (G) were created in the closed forest as a circular, small canopy gap with a diameter of 20 m.
- 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 cm³ 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 Hürka (1996); Lindroth (1985; 1986) and followed the taxonomy established by Hürka (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), Hürka (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 ($z_i \sim 1$), 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

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
<i>Abax parallelepipedus</i>	nbinom2	Intercept	228.586	1	<0.001
		Treatment	2.084	4	0.720
		Year	99.576	4	<0.001
		Treatment $\times$ Year	68.037	16	<0.001
<i>Aptinus bombarda</i>	nbinom2	Intercept	139.622	1	<0.001
		Treatment	2.033	4	0.730
		Year	81.402	4	<0.001
		Treatment $\times$ Year	44.767	16	<0.001
<i>Carabus coriaceus</i>	nbinom2	Intercept	5.638	1	0.035
		Treatment	2.820	4	0.588
		Year	102.798	4	<0.001
		Treatment $\times$ Year	38.445	16	0.004
<i>Carabus hortensis</i>	nbinom2	Intercept	151.766	1	<0.001
		Treatment	6.397	4	0.171
		Year	206.354	4	<0.001
		Treatment $\times$ Year	57.737	16	<0.001
<i>Carabus scheidleri</i>	genpois	Intercept	51.144	1	<0.001
		Treatment	5.909	4	0.206
		Year	17.577	4	0.004
		Treatment $\times$ Year	30.859	16	0.028
<i>Carabus ullrichii</i>	nbinom2	Intercept	3.489	1	0.185
		Treatment	3.590	4	0.464
		Year	40.817	4	<0.001
		Treatment $\times$ Year	16.373	16	0.464
<i>Nebria brevicollis</i>	genpois	Intercept	1.031	1	0.620
		Treatment	1.958	4	0.743
		Year	13.865	4	0.031
		Treatment $\times$ Year	22.400	16	0.392
<i>Pterostichus melanarius</i>	nbinom2	Intercept	10.212	1	0.004
		Treatment	3.254	4	0.516
		Year	15.671	4	0.007
		Treatment $\times$ 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

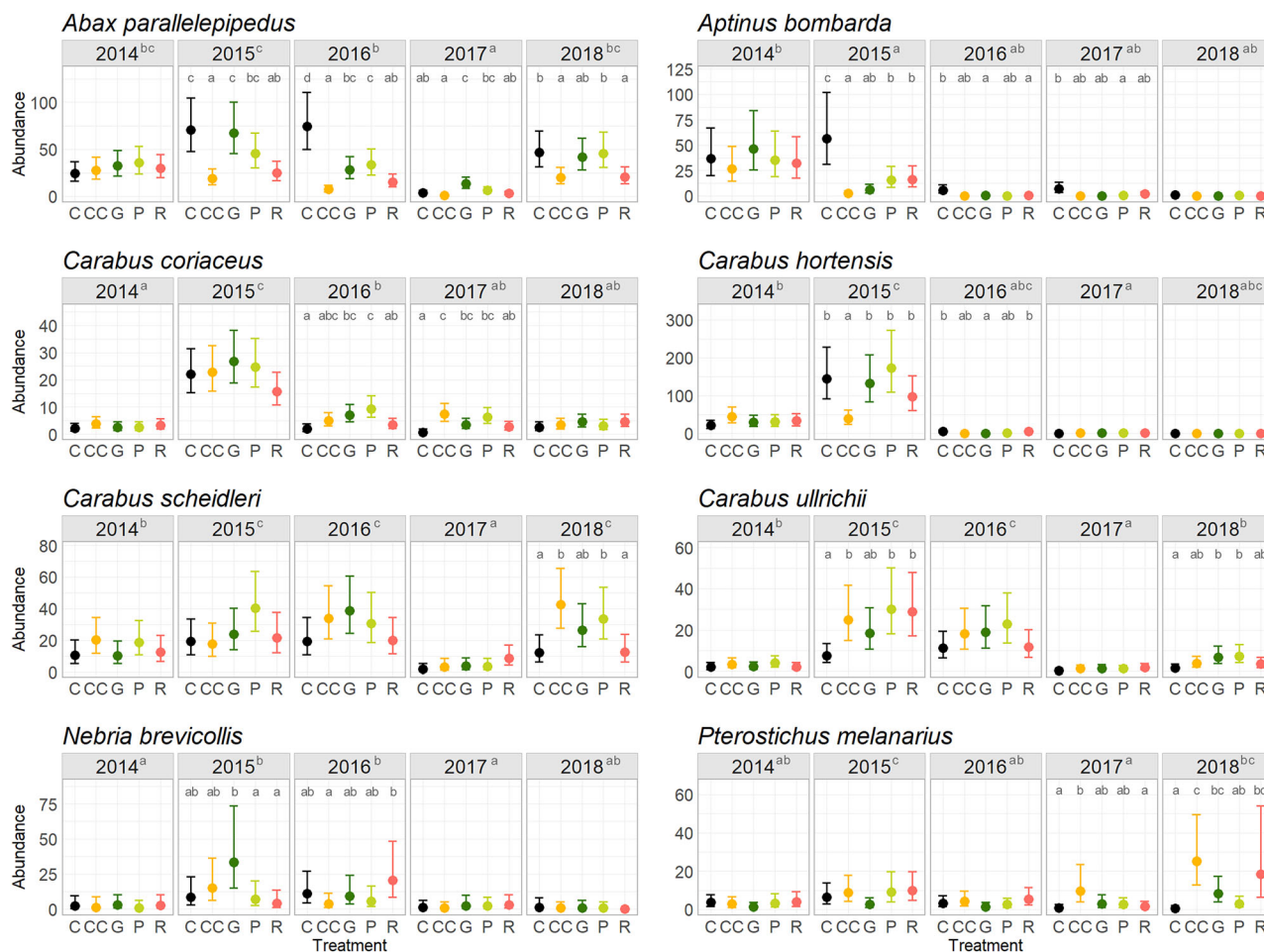


FIGURE 2 Estimated marginal means for species abundances across different treatments and years. The solid dots represent predicted means, and vertical lines indicate 95% confidence intervals. Different lowercase letters denote significant differences among treatments and years, based on Tukey's multiple 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,

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.

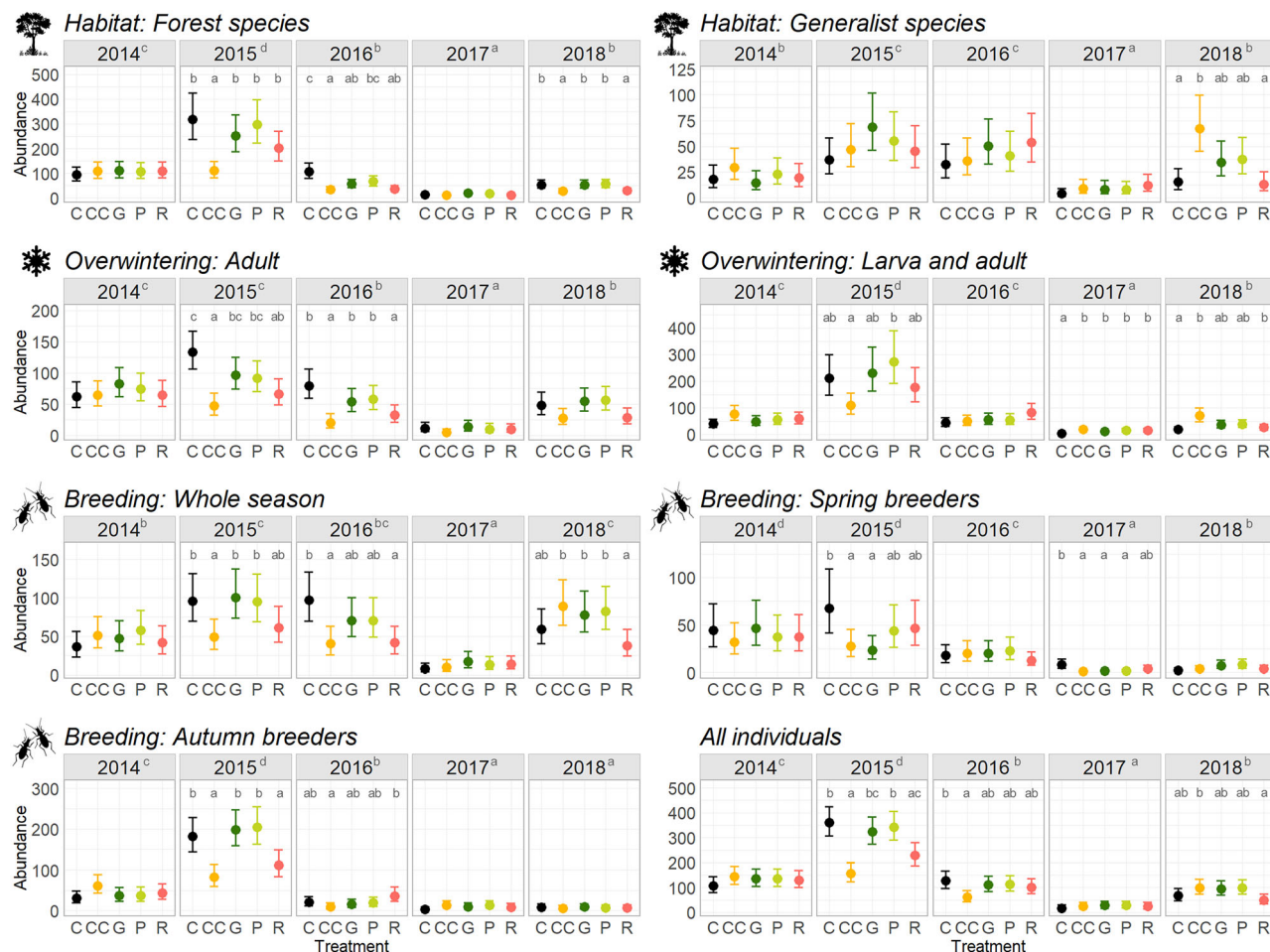


FIGURE 3 Estimated marginal means for trait-specific abundances and total abundance across different treatments and years. The solid dots represent predicted means, and vertical lines indicate 95% confidence intervals. Different lowercase letters denote significant differences among treatments and years, 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).

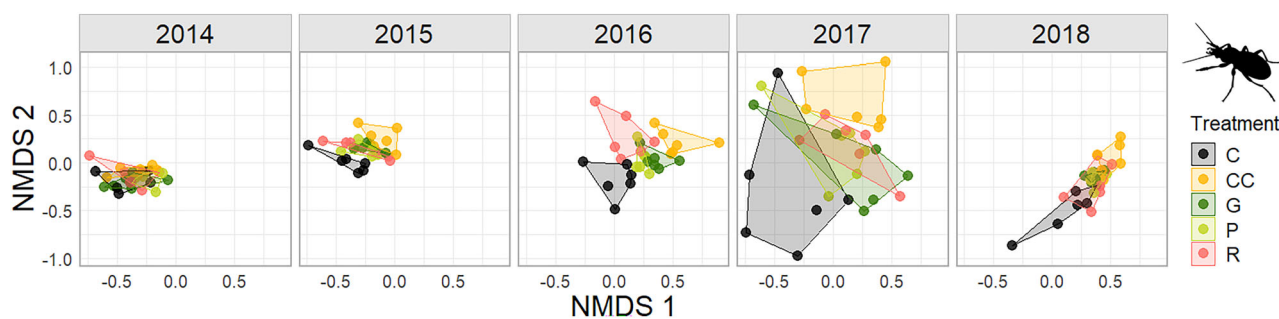


FIGURE 4 Non-metric multidimensional scaling (NMDS) biplots of eight carabid species captured across different forestry treatments and years using the Bray–Curtis dissimilarity matrix (overall stress value = 0.190). Points represent individual plots, and convex hulls delineate the treatment groups within 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

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 (Růžicková et al., 2021; Růžicková & 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. bombardica* 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

(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; Irmeler, 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, teners 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 Růžicková: 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.

DATA AVAILABILITY STATEMENT

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

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REFERENCES

- Andorkó, R. & Kádár, F. (2009) Life-history characteristics of the ground beetle *Carabus scheidleri* (Coleoptera: Carabidae) in Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae*, 55, 381–393.
- Aszalós, R., Thom, D., Aakala, T., Angelstam, P., Brūmelis, G., Gálhidy, L. et al. (2022) Natural disturbance regimes as a guide for sustainable Forest Management in Europe. *Ecological Applications*, 32, e2596.
- Bale, J.S. & Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of Experimental Biology*, 213, 980–994.
- Bartoň, K. (2024) MuMIn: Multi-Model Inference. <https://CRAN.R-project.org/package=MuMIn>
- Baumgartner, R., Bechtel, A., Van Den Boom, A., Hockmann, P., Horstmann, B., Klieve, V. et al. (1997) Age pyramid of a local population and viability fitness of phenotypical fractions in *Carabus auronitens* (Coleoptera, Carabidae). *The Italian Journal of Zoology*, 64, 319–340.
- Bengtsson, J., Nilsson, S.G., Franc, A. & Menozzi, P. (2000) Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*, 132, 39–50.
- Boggs, C.L. (2016) The fingerprints of global climate change on insect populations. *Current Opinion in Insect Science*, 17, 69–73.
- Boros, G., Kovács, B. & Ódor, P. (2019) Green tree retention enhances negative short-term effects of clear-cutting on enchytraeid assemblages in a temperate forest. *Applied Soil Ecology*, 136, 106–115.
- Brandmayr, P. & Pizzolotto, R. (2016) Climate change and its impact on epigeal and hypogean carabid beetles. *Periodicum Biologorum*, 118, 147–162.
- Brooks, D.R., Bajer, J.E., Clark, S.J., Monteith, D.T., Andrews, C., Corbett, S.J. et al. (2012) Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology*, 49, 1009–1019.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.
- Buckley, L.B. (2022) Temperature-sensitive development shapes insect phenological responses to climate change. *Current Opinion in Insect Science*, 52, 100897.
- Chamberlain, D., Gobbi, M., Negro, M., Caprio, E., Palestini, C., Pedrotti, L. et al. (2020) Trait-modulated decline of carabid beetle occurrence along elevational gradients across the European Alps. *Journal of Biogeography*, 47, 1030–1040.
- Cours, J., Bouget, C., Barsoum, N., Horák, J., Le Souchu, E., Leverkus, A.B. et al. (2023) Surviving in changing forests: abiotic disturbance legacy effects on arthropod communities of temperate forests. *Current Forestry Reports*, 9, 189–218.
- Didham, R.K., Basset, Y., Collins, C.M., Leather, S.R., Littlewood, N.A., Menz, M.H.M. et al. (2020) Interpreting insect declines: seven challenges and a way forward. *Insect Conservation and Diversity*, 13, 103–114.
- Dörfler, I., Gossner, M.M., Müller, J., Seibold, S. & Weisser, W.W. (2018) Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. *Biological Conservation*, 228, 70–78.
- Dövényi, Z. (2010) Magyarország kistájainak kataszttere. Magyar Földtani Intézet, Budapest, Hungary.
- Elek, Z., Kovács, B., Aszalós, R., Boros, G., Samu, F., Tinya, F. et al. (2018) Taxon-specific responses to different forestry treatments in a temperate forest. *Scientific Reports*, 8, 16990.
- Elek, Z., Ružičková, J. & Ódor, P. (2022) Functional plasticity of carabids can presume better the changes in community composition than taxon-based descriptors. *Ecological Applications*, 32, e02460.
- European Commission. (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of Wild Fauna and Flora. European Commission, Brussels, Belgium; Luxembourg City, Luxembourg. <http://data.europa.eu/eli/dir/1992/43/oj>
- Forrest, J.R. (2016) Complex responses of insect phenology to climate change. *Current Opinion in Insect Science*, 17, 49–54.
- Fournier, A.M., White, E.R. & Heard, S.B. (2019) Site-selection bias and apparent population declines in long-term studies. *Conservation Biology*, 33, 1370–1379.
- Fox, J. & Weisberg, S. (2018) *An R companion to applied regression*. Thousand Oaks, CA: Sage publications.
- Green, R.H. (1979) *Sampling design and statistical methods for environmental biologists*. New York, New York, USA: Wiley.
- Hartig, F., Lohse, L. & de Souza leite, M. (2024) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. <https://cran.r-project.org/package=DHARMa>
- Harvey, J.A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P.K. et al. (2023) Scientists' warning on climate change and insects. *Ecological Monographs*, 93, e1553.
- Heikkala, O., Seibold, S., Koivula, M., Martikainen, P., Müller, J., Thorn, S. et al. (2016) Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. *Forest Ecology and Management*, 359, 51–58.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, 13, 207–251.
- Hochberg, Y. (1988) A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, 75, 800–802.
- Homburg, K., Drees, C., Boutaud, E., Nolte, D., Schuett, W., Zumstein, P. et al. (2019) Where have all the beetles gone? Long-term study reveals carabid species decline in a nature reserve in northern Germany. *Insect Conservation and Diversity*, 12, 268–277.
- Hürka, K. (1996) *Carabidae of the Czech and Slovak republics*. Zlin, Czech Republic: Kabourek.
- Irmeler, U. (2022) Seasonal shift in carabid phenology over a period of 18 years. *European Journal of Entomology*, 119, 183–190.
- Jactel, H., Koricheva, J. & Castagneyrol, B. (2019) Responses of forest insect pests to climate change: not so simple. *Current Opinion in Insect Science*, 35, 103–108.
- Jung, J.K., Lee, S.K., Lee, S.I. & Lee, J.H. (2018) Trait-specific response of ground beetles (Coleoptera: Carabidae) to forest fragmentation in the temperate region in Korea. *Biodiversity and Conservation*, 27, 53–68.
- Koivula, M., Kukkonen, J. & Niemelä, J. (2002) Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation*, 11, 1269–1288.
- Koivula, M.J., Venn, S., Hakola, P. & Niemelä, J. (2019) Responses of boreal ground beetles (Coleoptera, Carabidae) to different logging regimes ten years post harvest. *Forest Ecology and Management*, 436, 27–38.
- Kotze, D.J. & O'hara, R.B. (2003) Species decline—but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, 135, 138–148.

- Kovács, B., Tinya, F., Németh, C. & Ódor, P. (2020) Unfolding the effects of different forestry treatments on microclimate in oak forests: results of a 4-yr experiment. *Ecological Applications*, 30, e02043.
- Lange, M., Türke, M., Pašalić, E., Boch, S., Hessenmöller, D., Müller, J. et al. (2014) Effects of forest management on ground-dwelling beetles (Coleoptera: Carabidae, Staphylinidae) in Central Europe are mainly mediated by changes in forest structure. *Forest Ecology and Management*, 329, 166–176.
- Lenth, R. (2025) emmeans: Estimated Marginal Means, aka Least-Squares Means. <https://rvlenth.github.io/emmeans/>
- Lindenmayer, D.B., Franklin, J.F., Löhmus, A., Baker, S.C., Bauhus, J., Beese, W. et al. (2012) A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters*, 5, 421–431.
- Lindroth, C.H. (1985) The Carabidae (Coleoptera) of Fennoscandia and Denmark, part I. Fauna Entomologica Scandinavica. E.J. Brill, Leiden, The Netherlands.
- Lindroth, C.H. (1986) The Carabidae (Coleoptera) of Fennoscandia and Denmark, Part II. Fauna Entomologica Scandinavica, 15, part 2. E.-J. Brill, Leiden, The Netherlands.
- Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, 41, 231–256.
- Magura, T. & Lövei, G.L. (2019) Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland. *Insect Science*, 26, 154–163.
- Magura, T. & Lövei, G.L. (2024) Edge history modulates the depth of edge influence: evidence from ground beetles with different feeding traits. *Forest Ecology and Management*, 561, 121874.
- Magura, T., Tóthmérész, B. & Elek, Z. (2003) Diversity and composition of carabids during a forestry cycle. *Biodiversity and Conservation*, 12, 73–85.
- Marrec, R., Le Roux, V., Martin, L., Lenoir, J., Brunet, J., Cousins, S.A. et al. (2021) Multiscale drivers of carabid beetle (Coleoptera: Carabidae) assemblages in small European woodlands. *Global Ecology and Biogeography*, 30, 165–182.
- Mason, W.L., Diaci, J., Carvalho, J. & Valkonen, S. (2022) Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. *Forestry: An International Journal of Forest Research*, 95, 1–12.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14, 450–453.
- Murray, B.D., Holland, J.D., Summerville, K.S., Dunning, J.B., Jr., Saunders, M.R. & Jenkins, M.A. (2017) Functional diversity response to hardwood forest management varies across taxa and spatial scales. *Ecological Applications*, 27, 1064–1081.
- Negro, M., Vacchiano, G., Berretti, R., Chamberlain, D.E., Palestini, C., Motta, R. et al. (2014) Effects of forest management on ground beetle diversity in alpine beech (*Fagus sylvatica* L.) stands. *Forest Ecology and Management*, 328, 300–309.
- Nolte, D., Boutaud, E., Kotze, D.J., Schuldt, A. & Assmann, T. (2019) Habitat specialization, distribution range size and body size drive extinction risk in carabid beetles. *Biodiversity and Conservation*, 28, 1267–1283.
- Nolte, D., Schuldt, A., Gossner, M.M., Ulrich, W. & Assmann, T. (2017) Functional traits drive ground beetle community structures in central European forests: implications for conservation. *Biological Conservation*, 213, 5–12.
- O'Hara, K.L. (2016) What is close-to-nature silviculture in a changing world? *Forestry*, 89, 1–6.
- Oksanen, J. (2025) vegan: community ecology package. <https://cran.r-project.org/package=vegan>
- Paillet, Y., Bergés, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M. et al. (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology*, 24, 101–112.
- Pommerening, A. & Murphy, S.T. (2004) A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry*, 77, 27–44.
- Pro Silva. (2012) Pro Silva Principes. Pro Silva – Association of European Foresters Practicing Management which follows Natural Processes.
- R Core Team. (2023) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from: <https://www.R-project.org/>
- Růžicková, J., Bérces, S., Ackov, S. & Elek, Z. (2021) Individual movement of large carabids as a link for activity density patterns in various forestry treatments. *Acta Zoologica Academiae Scientiarum Hungaricae*, 67, 77–86.
- Růžicková, J. & Veselý, M. (2018) Movement activity and habitat use of *Carabus ullrichii* (Coleoptera: Carabidae): the forest edge as a mating site? *Entomological Science*, 21, 76–83.
- Samu, F., Elek, Z., Kovács, B., Fülöp, D., Botos, E., Schmera, D. et al. (2021) Resilience of spider communities affected by a range of silvicultural treatments in a temperate deciduous forest stand. *Scientific Reports*, 11, 20520.
- Samu, F., Elek, Z., Růžicková, J., Botos, E., Kovács, B. & Ódor, P. (2023) Can gap-cutting help to preserve Forest spider communities? *Diversity*, 15, 240.
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D. et al. (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, 55, 267–278.
- Schleuning, M., Neuschulz, E.L., Albrecht, J., Bender, I.M., Bowler, D.E., Dehling, D.M. et al. (2020) Trait-based assessments of climate-change impacts on interacting species. *Trends in Ecology & Evolution*, 35, 319–328.
- Sitzia, T., Campagnaro, T., Gatti, E., Sommacal, M. & Kotze, D.J. (2015) Wildlife conservation through forestry abandonment: responses of beetle communities to habitat change in the eastern Alps. *European Journal of Forest Research*, 134, 511–524.
- Staab, M., Gossner, M.M., Simons, N.K., Achury, R., Ambarli, D., Bae, S. et al. (2023) Insect decline in forests depends on species' traits and may be mitigated by management. *Communications Biology*, 6, 338.
- Staab, M. & Schuldt, A. (2020) The influence of tree diversity on natural enemies – a review of the “enemies” hypothesis in forests. *Current Forestry Reports*, 6, 243–259.
- Sultaire, S.M., Kroll, A.J., Verschuyt, J., Landis, D.A. & Roloff, G.J. (2021) Effects of varying retention tree patterns on ground beetle (Coleoptera: Carabidae) taxonomic and functional diversity. *Ecosphere*, 12, e03641.
- Thiele, H.U. (1977) *Carabid beetles in their environments*. New York, USA: Springer.
- Tinya, F., Kovács, B., Aszalós, R., Tóth, B., Csépanyi, P., Németh, C. et al. (2020) Initial regeneration success of tree species after different forestry treatments in a sessile oak-hornbeam forest. *Forest Ecology and Management*, 459, 117810.
- Turin, H., Penev, L. & Casale, A. (2003) The genus *Carabus* in Europe, a synthesis. Fauna Europea Invertebrata. Pensoft, Sofia, Bulgaria.
- Van Dyck, H., Bonte, D., Puls, R., Gotthard, K. & Maes, D. (2015) The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos*, 124, 54–61.
- Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. & Stopak, D. (2021) Insect decline in the Anthropocene: death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2023989118.
- Weiss, F., von Wehrden, H. & Linde, A. (2024) Long-term drought triggers severe declines in carabid beetles in a temperate forest. *Ecography*, 2024, e07020.

- Weiss, F., Winter, S., Pflugmacher, D., Kolling, T. & Linde, A. (2024) Evidence for regional-scale declines in carabid beetles in old lowland beech forests following a period of severe drought. *Landscape Ecology*, 39, 123.
- White, E.R. (2019) Minimum time required to detect population trends: the need for long-term monitoring programs. *Bioscience*, 69, 40–46.
- Yadav, B., Jeyaseelan, L., Jeyaseelan, V., Durairaj, J., George, S., Selvaraj, K.G. et al. (2021) Can generalized Poisson model replace any other count data models? An evaluation. *Clinical Epidemiology and Global Health*, 11, 100774.
- Yamanaka, S., Yamaura, Y., Sayama, K., Sato, S. & Ozaki, K. (2021) Effects of dispersed broadleaved and aggregated conifer tree retention on ground beetles in conifer plantations. *Forest Ecology and Management*, 489, 119073.

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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