

Surface temperature and shrub cover drive ground beetle (Coleoptera: Carabidae) assemblages in short-rotation coppices

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- Abstract**
- 1 Increasing demand for biomass has led to an on-going intensification of fuel wood plantations with possible negative effects on open land biodiversity. Hence, ecologists increasingly call for measures that reduce those negative effects on associated biodiversity. However, our knowledge about the efficiency of such measures remains scarce.
 - 2 We investigated the effects of gap implementation in short rotation coppices (SRCs) on carabid diversity and assemblage composition over 3 years, with pitfall traps in gaps, edges and interiors. In parallel, we quantified soil surface temperature, shrub- and herb cover.
 - 3 Edges had the highest number of species and abundances per trap, whereas rarefied species richness was significantly lower in short rotation coppice interiors than in other habitat types. Carabid community composition differed significantly between habitat types. The main environmental drivers were temperature for number of species and abundance and shrub cover for rarefied species richness.
 - 4 We found significantly higher rarefied species richness in gaps compared with interiors. Hence, we argue that gap implementation benefits overall diversity in short rotation coppices. Furthermore, the differences in species community composition between habitat types through increased species turnover support carabid diversity in short rotation coppices. These positive effects were largely attributed to microclimate conditions. However, to maintain positive effects, continuous management of herb layer might be necessary.

Keywords Carabidae, fuel wood, short-rotation coppice, shrub-cover, temperature.

Introduction

Biomass has become an important source of renewable energy during the last decades and is predicted to gain importance in the coming decades (Schulz *et al.*, 2009). Higher demand of biomass cannot only be compensated by additional forest harvesting (Döpke *et al.*, 2013). Therefore, fast growing trees are increasingly grown as short-rotation coppices (SRC) on agricultural land. Due to the higher growth rate of juvenile trees, SRCs show higher productivity of wood than conventional forestry (Baum *et al.*, 2009) and can regularly be coppiced (2–8 years rotation) at the ground level (Vanbeveren & Ceulemans, 2019).

Widespread arthropod declines have occurred in recent years (Seibold *et al.*, 2019). In open habitats, those declines are driven

by land-use intensification often coupled with an increase in the proportion of agricultural land in the landscape (Seibold *et al.*, 2019).

An increase of SRC plantations is expected (Baum *et al.*, 2009) and scientific studies provide mixed results about their effects on biodiversity, when compared to arable fields. Research studies examining the effects of SRCs on biodiversity have generally reported positive effects for mammals (Campbell *et al.*, 2014), birds (Berg, 2002; Sage *et al.*, 2006; Riffell *et al.*, 2011), earthworms (Makeschin *et al.*, 1989; Schrama *et al.*, 2014) and arthropods (Sage, 1998; Reddersen, 2001; Blick *et al.*, 2003; Verheyen *et al.*, 2014). Although SRCs mostly host higher species richness of insects than arable fields (Rowe *et al.*, 2011), several scientific studies suggest that carabid diversity is negatively affected (Ward & Ward, 2001; Allegro & Sciaky, 2003; Liesebach & Mecke, 2003; Britt *et al.*, 2007; Lamersdorf *et al.*, 2008).

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Carabid species vary in their habitat demands and can therefore be useful indicators of changes in habitat quality (Lövei & Sunderland, 1996; Niemelä *et al.*, 2000). Their taxonomy, especially in Europe, is well documented and much is known about behaviour and habitat requirements (Thiele, 1977). A majority of carabids are predators and therefore not tied to specific plant species. Their distribution, abundance and diversity are affected by biotic factors like abundance of prey and vegetation structure (Siemann *et al.*, 1998; Brose, 2003), as well as microclimatic conditions such as moisture, temperature and light regime (Thiele, 1977; Koivula *et al.*, 1999).

The opposing results between carabids and other studied animal groups indicate that the effects of SRCs on biodiversity may strongly depend on heterogeneity and spatial structure of the SRC (Schulz *et al.*, 2009). On a landscape level, SRCs could negatively affect biodiversity in forest-dominated landscapes, but have a high potential enhancing biodiversity in structurally homogenous agricultural-dominated landscapes (Vanbeveren & Ceulemans, 2019). Yet, it remains unclear how within SRC characteristics, such as ground vegetation cover or associated soil surface temperature, affect the composition of carabid assemblages.

One potential measure to reduce potential negative effects of SRCs on carabids would be to create gaps within plantations. Gaps could benefit carabid diversity in coppices, due to introduction of open habitat species, which for carabids are generally more diverse than forest species (Niemelä & Halme, 1992; Halme & Niemelä, 1993; Magura *et al.*, 2001; Koivula *et al.*, 2004; Roume *et al.*, 2011). Furthermore, gaps would help to increase heterogeneity, utilize edge effects and create a higher variety of influences that affect carabid diversity, such as light, temperature and differences in ground vegetation. Higher edge-to-area ratio to support biodiversity in SRCs was previously recommended by Rowe *et al.* (2007) and Vanbeveren & Ceulemans (2019), but there remains little direct evidence of the efficacy of this approach for promoting carabid diversity.

Our study aims to quantify the effects of creating gaps in SRCs on carabid diversity. We hypothesize that (i) gaps in SRCs will have higher carabid species richness than interiors, due to high dispersal power of open habitat species and generalists, (ii) temperature will be the main driver for higher carabid species richness in gaps, partially due to increased activity in higher temperatures and (iii) carabid species richness will be the highest in SRC edges, by combining species assemblages from SRCs and adjacent fields. To test these hypotheses, we collected carabids in SRC interiors, gaps and edges between 2013 and 2015.

Material and methods

Study area and study design

The study was conducted in the vicinity of Haine (N 51:2:22.024, W 8:43:16.831, DMS WGS 84) in the state of Hesse in Germany (Fig. 1). The climate in the region is temperate with an average annual temperature of 8.5 °C and average annual precipitation of 818 mm (www.climate-data.org). Soil type in the area is mostly brown earth with loamy sand to sandy loam (www.bodenviewer.hessen.de).

SRCs were first established in 2008 and 2009. Most plots (9 of 12) were harvested once prior (five plots in 2010, three in 2012) or during our study (one plot in 2014). SRC stand ages ranged from 1 to 4 years after last harvest, with a planned rotation cycle of approximately 4 years.

Sampling took place in three different habitat types of SRCs. Sampled habitat types were (i) inside the short-rotation coppice (interior), (ii) within gaps inside the short rotation coppice (gap) and (iii) on the edges outside the short-rotation coppice (edge). Among these habitat types, 14 plots were selected (initially six interior plots, six gap plots, two edge plots) and at each plot four pitfall traps were placed in a transect with 7 m between traps. Gaps consisted out of sites where poplar plants failed to root after planting (Fig. 1). Therefore, gaps had no concrete size and showed variations between approximately 100–350 m². Traps were placed in a central transect within gaps. Traps on edges were placed on transects alongside SRC edge with a distance of 5 m. Different habitat types are illustrated in Fig. 1. One interior plot was harvested after the first sampling period and was thereafter attributed as habitat type gap for the following two sampling periods. For analyses, this plot was treated as interior in 2013 and afterwards as gap. Therefore, only five interior and seven gap plots appear in Fig. 1, as it was in 2014 and 2015. Mean distances between the plots were 375 m with a minimum of 16 m and a maximum of 798 m. We tested for possible spatial autocorrelation due to the clustered design, however no special dependencies were detected.

We sampled carabids between June and September in 2013, 2014 and 2015. Due to personal and financial constraints, 20 of the total 56 traps could only be sampled in one of the 3 years, resulting in 128 total samples (48 interior, 56 gap, 24 edge). Traps were emptied in 4-week intervals. Pitfall traps consisted of 370 mL glass jars with an inner diameter of 5.5 cm and were covered with a 20 by 20 cm acrylic glass roof as protection against rain and leaf-litter. Trapping solution was a 10% sodium benzoate solution, acidified to a pH of about 6, with an added odourless detergent to reduce surface tension. Carabids were identified according to Müller-Motzfeld (2004), following the nomenclature of Löbl & Löbl (2017).

We measured soil temperature, herb cover, and shrub cover. Soil temperature was recorded using *LogTag* data-loggers from CiK Solutions GmbH closely below soil surface in 1–2 cm depth, next to traps 1 and 4 of every plot. Temperature was recorded hourly and the mean temperature was calculated per plot and year for all trapping days to serve as a predictor in the following analyses. Herb cover (herbaceous plants <1.2 m height) and shrub cover (herbaceous and woody plants >1.2 m) were estimated in steps of 10% on first July of every year within 1 m² around each trap.

To provide deeper insight into which types of carabids are favoured by different habitat types, we selected three ecological traits to distinguish carabid types through their ecological preferences and dispersal ability. We selected their forest preference ranging from 1 (strong preference for open habitats) to 7 (strong preference for closed forests), and humidity preference ranging from 1 (species predominantly found in dry habitats) to 10 (species predominantly found in wet habitats) as indicators for ecological preferences in habitat selection. Furthermore, we selected flight ability as a proxy of dispersal ability ranging from

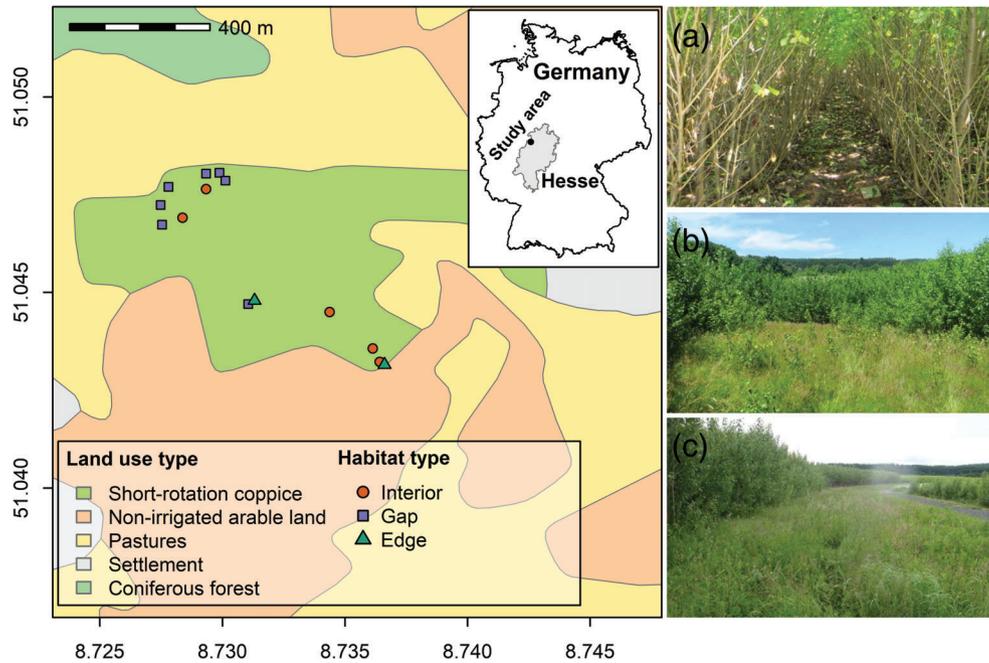


Figure 1 Location of the study plots divided into different habitat types. Background shows land cover classes taken from Copernicus CORINE land cover 2018 (EEA, 2018). Inset map shows the location of the study area in Germany and the state Hesse. Habitat types are illustrated on the right-hand side of the map with (a) showing interior, (b) showing gap and (c) showing edge.

1 (not able to fly) to 3 (able to fly) to test if dispersal ability may hinder species from colonizing gaps inside SRCs (see Table S1 for a full list of traits with their affiliated literature sources and Table S2 for a full list of species with their affiliated traits).

Data analysis

All statistical analyses were carried out in R 3.6.2 (R Core Team, 2018) and were performed on trap level. The samples were pooled per trap and year. Sampling efforts varied between different habitat types and years, therefore we used rarefaction of incidence frequencies to the smallest actual sample size by means of the *iNEXT* package (Hsieh *et al.*, 2016) for comparison. Furthermore, we use the term species density, defined as the actual number of observed species per sampling unit. When referring to the results of sample-based rarefaction, conducted with the *rarefy* command of the *vegan* package (Oksanen *et al.*, 2012), we use the term species richness, referring to data standardized to a common number of individuals, as proposed by Gotelli and Colwell (2001).

We applied nonmetric multidimensional scaling (NMDS) using the function *metaMDS* in the package *vegan* (Oksanen *et al.*, 2012) to visualize the differences in community composition between habitat types. Environmental variables were fitted to the ordination using the function *envfit* with 1000 permutations. To identify indicator species for different habitat types, we used a multi-level pattern analysis from the *indicspecies* package (De Cáceres & Legendre, 2009) and corrected *p* values for pairwise combinations using *Benjamini & Hochberg* correction. Additionally, to support the results of indicator species, the similarity percentages as proposed by Clarke (1993) were calculated

to identify the contribution of individual species to the overall community dissimilarities between habitat types, using the *simper* function in the *vegan* package (Table S3). We used permutational multivariate analysis of variance, provided by the *adonis2* function in the *vegan* package (Oksanen *et al.*, 2012), for all pairwise combinations of different habitat types and adjusted *p* values with *Bonferroni* correction.

To test for the effects of herb cover, shrub cover and soil temperature, we fitted generalized linear mixed-effect models with Poisson error distribution for count data (species density and abundance) and Gaussian error distribution for species richness as response variables. To account for temporal and spatial re-sampling, we added the trap location and the study year as random effects to the model formula. We added an observation-specific random effect to the abundance model to account for possible Poisson-overdispersion (Elston *et al.*, 2001).

To test for significant differences of response variables between habitat types, environmental variables were replaced in the linear mixed-effect models with habitat type as predictor. We then applied multiple comparisons with adjustment of *p* values by a simultaneous inference procedure provided by the *glht* function in the *multcomp* package (Hothorn *et al.*, 2008). The same procedure was then used to test for influences of habitat type on community weighted trait means. The community weighted means were calculated for each of the three selected traits of the species per trap and habitat type.

We used bootstrap spline-correlograms with the *spline.correlog* function in the *ncf* package (Bjørnstad & Falck, 2001) to inspect all model residuals for possible spatial autocorrelation. However, we did not detect any spatial dependency in our model outputs (Fig. S1).

Table 1 Species list with total abundance and abundances respective to their habitat types

Subfamily	Tribe	Species	Interior	Gap	Edge	Total		
Carabinae	Carabini	<i>Carabus violaceus</i>	436	130	199	765		
		<i>Carabus problematicus</i>	1	0	0	1		
		<i>Carabus granulatus</i>	1	6	1	8		
		<i>Carabus auratus</i>	1	0	0	1		
		<i>Carabus nemoralis</i>	15	9	3	27		
Nebrinae	Nebriini	<i>Leistus ferrugineus</i>	10	31	11	52		
		<i>Nebria brevicollis</i>	375	50	57	482		
	Notiophilini	<i>Notiophilus palustris</i>	4	9	12	25		
		<i>Notiophilus biguttatus</i>	49	6	11	66		
Loricarinae	Loricerini	<i>Loricera pilicornis</i>	42	17	18	77		
Scaritinae	Clivinini	<i>Clivina fossor</i>	21	52	67	140		
		<i>Dyschirius globosus</i>	0	1	0	1		
Trechinae	Trechini	<i>Epaphius secalis</i>	2	29	1	32		
		<i>Trechus quadristriatus</i>	18	21	69	108		
		<i>Trechus obtusus</i>	0	9	0	9		
		<i>Trechoblemus micros</i>	1	4	0	5		
	Bembidiini	<i>Bembidion lampros</i>	427	262	757	1446		
		<i>Bembidion properans</i>	0	1	0	1		
		<i>Bembidion gilvipes</i>	0	0	1	1		
		<i>Bembidion quadrimaculatum</i>	0	4	3	7		
		<i>Bembidion obtusum</i>	7	3	5	15		
		<i>Bembidion mannerheimii</i>	0	4	0	4		
		<i>Bembidion lunulatum</i>	0	21	0	21		
		<i>Asaphidion flavipes</i>	0	3	4	7		
		Harpalinae	Harpalini	<i>Anisodactylus binotatus</i>	0	5	5	10
				<i>Diachromus germanus</i>	0	1	0	1
				<i>Trichotichnus laevicollis</i>	0	1	1	2
<i>Trichotichnus nitens</i>	3			1	0	4		
<i>Harpalus rufipes</i>	152			218	417	787		
<i>Harpalus affinis</i>	11			76	159	246		
<i>Harpalus latus</i>	34			169	50	253		
<i>Harpalus rubripes</i>	3			7	7	17		
<i>Harpalus tardus</i>	0			0	3	3		
<i>Ophonus rufibarbis</i>	0			2	3	5		
<i>Bradycellus harpalinus</i>	0			3	1	4		
<i>Bradycellus csikii</i>	4			7	23	34		
Pterostichini	<i>Stomis pumicatus</i>			17	1	1	19	
	<i>Poecilus cupreus</i>			33	27	217	277	
	<i>Poecilus versicolor</i>		104	586	763	1453		
	<i>Pterostichus strenuus</i>	76	25	19	120			
	<i>Pterostichus diligens</i>	0	0	1	1			
	<i>Pterostichus vernalis</i>	73	58	102	233			
	<i>Pterostichus oblongopunctatus</i>	5	2	1	8			
	<i>Pterostichus niger</i>	1388	766	251	2405			
	<i>Pterostichus melanarius</i>	715	459	476	1650			
	<i>Abax parallelepipedus</i>	87	45	1	133			
	<i>Abax ovalis</i>	1	1	0	2			
Sphodrini	<i>Synuchus vivalis</i>	12	5	18	35			
	<i>Calathus fuscipes</i>	2	32	32	66			
	<i>Calathus melanocephalus</i>	1	13	49	63			
Platynini	<i>Calathus rotundicollis</i>	1	0	0	1			
	<i>Olisthopus rotundatus</i>	0	2	1	3			
	<i>Agonum sexpunctatum</i>	2	15	4	21			
	<i>Agonum muelleri</i>	10	7	8	25			
	<i>Agonum fuliginosum</i>	1	5	1	7			
	<i>Anchomenus dorsalis</i>	444	159	955	1558			
	<i>Limodromus assimilis</i>	351	34	6	391			
	<i>Oxypselaphus obscurus</i>	75	60	19	154			

Table 1 Continued

Subfamily	Tribe	Species	Interior	Gap	Edge	Total
	<i>Zabrinini</i>	<i>Amara plebeja</i>	4	102	76	182
		<i>Amara similata</i>	1	0	2	3
		<i>Amara ovata</i>	0	0	4	4
		<i>Amara montivaga</i>	1	0	3	4
		<i>Amara convexior</i>	0	3	2	5
		<i>Amara communis</i>	1	12	237	250
		<i>Amara lunicollis</i>	1	96	46	143
		<i>Amara aenea</i>	1	10	2	13
		<i>Amara eurynota</i>	1	0	1	2
		<i>Amara familiaris</i>	0	14	5	19
		<i>Amara cursitans</i>	0	0	4	4
		<i>Amara bifrons</i>	2	0	10	12
		<i>Amara consularis</i>	8	1	7	16
		<i>Amara aulica</i>	6	12	549	567
		<i>Chlaeniini</i>	<i>Chlaenius nigricornis</i>	0	0	1
	<i>Licinini</i>	<i>Badister bullatus</i>	7	22	3	32
		<i>Badister lacertosus</i>	4	0	0	4
	<i>Panagaeini</i>	<i>Panagaeus cruxmajor</i>	11	18	56	85
		<i>Panagaeus bipustulatus</i>	0	1	4	5
	<i>Lebiini</i>	<i>Demetrias atricapillus</i>	1	0	0	1
<i>Brachininae</i>	<i>Brachinini</i>	<i>Brachinus crepitans</i>	12	12	438	462
Total			5076	3767	6263	15 106

Sample size of each habitat was 48 for interior, 56 for gaps and 24 for edges.

Results

A total of 15 106 carabids were identified belonging to 35 genera and 79 species. A full list of recorded species with total abundance and abundances respective to their habitat type is displayed in Table 1. Most abundant species were *Pterostichus niger* (Schaller, 1783) (15.9%), *Pterostichus melanarius* (Illiger, 1798) (10.9%) and *Anchomenus dorsalis* (Pontoppidan, 1763) (10.3%). The highest gamma diversity was found in edges (65 species), followed by gaps (64) and interiors (57), as indicated by rarefaction (Fig. 2a). However, we found no significant differences in species richness between years (Fig. 2b).

Species density was significantly higher in edges (22.0 median), compared with interiors (15.0) and gaps (13.5). Interiors and gaps showed no significant difference between each other (Fig. 3a). Abundance significantly varied between all habitat types (Fig. 3b). The highest abundance was observed in edges (191.5 median), followed by interiors (74.5). The lowest abundances were recorded in gaps (54.5). Species richness was significantly lower in interiors (5.16 median) than in gaps (5.28) and edges (5.96, Fig. 3c).

The composition of carabid species assemblage differed between habitat types (Fig. 4). The results of permutational multivariate analysis revealed significant differences in carabid assemblage composition among all study years and between all different habitat types (Table S4). However, the lesser variability of species assemblages in edges compared with interiors and gaps can at least partially be attributed to a smaller sample size. The overall species composition was driven by temperature, year, herb- and shrub cover. We found six species unique to edge, six species unique to gap and five species unique to interior. All species unique to a single habitat type were rare,

meaning they did not reach 1% dominance in their respective assemblages. Indicator species analysis confirmed differences between habitat types, with seven characteristic indicator species for short-rotation coppice, two for gaps and 26 for edges (Fig. 4). The results of indicator species are supported by calculated contributions of species for overall dissimilarities between habitat types (Table S3).

Carabids in edges were less bound to forest habitats, especially compared with interiors, whereas gaps showed intermediate values (Fig. 5a). Carabids in edges preferred habitats with dryer conditions than in carabids in interiors, while assemblages in gaps showed intermediate values (Fig. 5b). Furthermore, carabids in interiors had a significantly lower dispersal ability than carabid assemblages in gaps and edges (Fig. 5c). The results from linear mixed-effect models are displayed in Table S5.

Declines of abundances of open habitat species were noticeable in interiors but interestingly also in edges. A steady decline of abundance over the course of the three sampling periods in 2013, 2014 and 2015 was observed in edges for *A. dorsalis* (794, 138 and 23), *Brachinus crepitans* (Linnaeus, 1758) (294, 141 and 3), *Harpalus rufipes* (De Geer, 1774) (308, 62 and 47) and *Harpalus affinis* (Schränk, 1781) (126, 27 and 6). Furthermore, species density decreased over the course of the 3-year sampling period from 2013 to 2015 in edges (53, 46 and 40) and interiors (48, 38 and 33), whereas it increased in gaps (45, 47 and 50). Especially in edges herb cover showed strong positive correlation with year (Pearson's r : -0.76 interior, -0.08 gap and 0.35 edge), while correlation of year and shrub cover was the strongest in interiors (Pearson's r : 0.69 interior, 0.54 gap and 0.42 edge).

Generalized mixed-effects models revealed a significant increase in species density and abundance with increasing temperature (Fig. 6a,b), whereas increasing shrub cover led

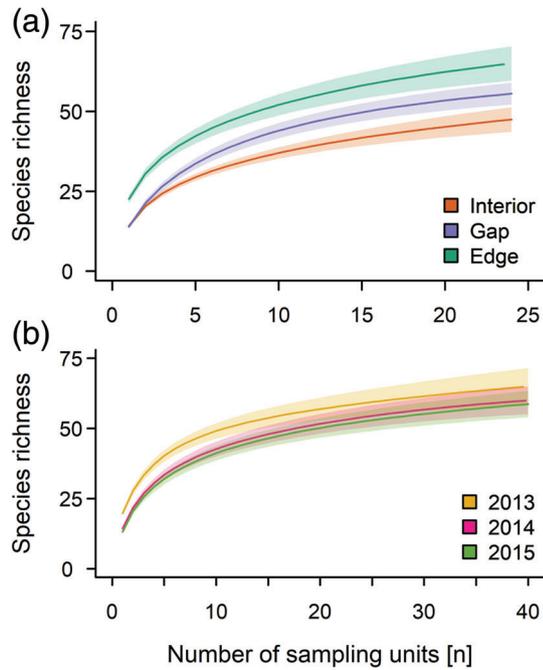


Figure 2 Sampling-unit-based incidence frequency rarefaction for (a) habitat types and (b) years. Sample units were taken from trap level individually for each year, resulting in 24 samples for edges 56 for gaps and 48 for interiors. Endpoint was set at the lowest sampling effort. Shaded band depicts 95% confidence intervals based on 50 bootstrap replicates.

to a decrease in species richness (Fig. 6c). Unlike results for community composition, herb cover had no significant effects on any response variable (Table 2).

According to the z -values in our models, temperature (2.20) was the more important driver compared with shrub cover (-0.80) for carabid species density and abundance (3.01 temperature, 1.49 shrub cover). For species richness, shrub cover (-2.11) had a stronger effect than temperature (1.54, see Table 2). The correlations between predictor variables range between min. -0.58 and max. 0.33 and are displayed in Table S6.

Discussion

Species richness was significantly higher in gaps than interiors, although corresponding abundances were lower. Edges hosted significantly higher species density, abundance and species richness than interiors. Species density and abundance were driven by temperature, although the main driver for species richness was shrub cover. Differences in environmental variables, like temperature, shrub and herb cover, significantly affected carabid species composition. Gamma-diversity in gaps was higher than in interiors and only slightly lower than in edges (Fig. 2). We therefore argue that differences in species compositions between gaps and interiors, as well as higher edge-to-area ratio, can lead to higher overall diversity in SRCs. This finding is supported by our results of trait analysis, showing that forest preference, humidity preference and dispersal ability of community weighted means of carabids from gaps show mostly intermediate values from interiors

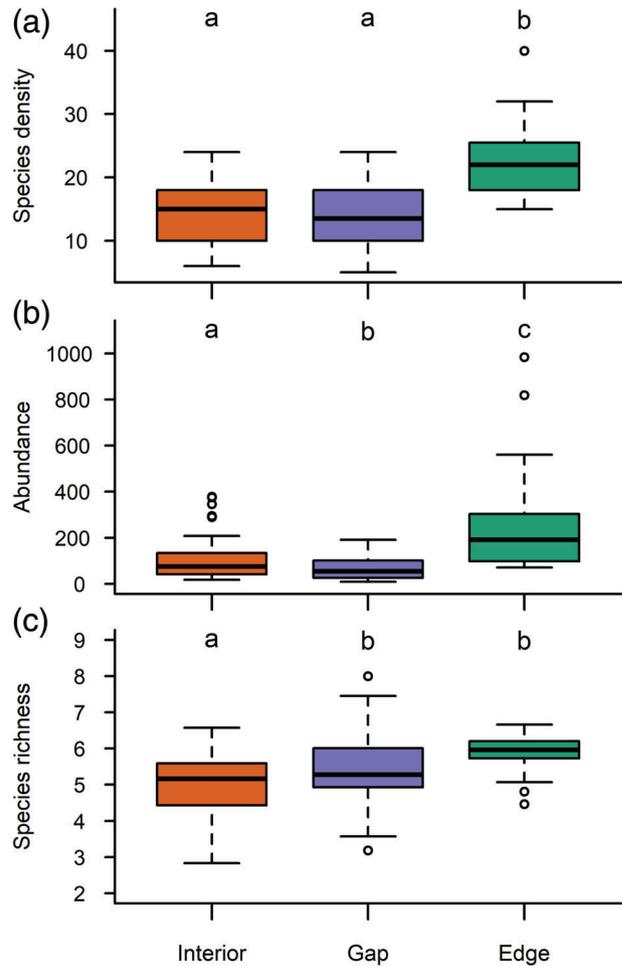


Figure 3 (a) Species density, (b) abundance and (c) species richness of all different habitat types on trap level per year. Small letters indicate significant differences ($P < 0.05$) between habitat types, resulting from generalized mixed-effect models with habitat type as predictor.

and edges. Gaps are therefore allowing co-occurrence of open habitat and forest species.

Influence of habitat type on species assemblages

The differences in species assemblages between habitat types are evident when portraying indicator species identified by multi-level pattern analysis and species with high dominance in their respective habitat types. Darker and more humid conditions in SRCs displaced open habitat species towards edges and gaps. This was evident for species like *A. dorsalis*, which was identified as an indicator species for edges. *A. dorsalis* is an open habitat species often found on agricultural land, other open habitats or forest edges, if they are not too shady or humid (Trautner, 2017). It was also the most common species found overall by Mader *et al.* (2017) when comparing flowering with cereal fields.

Due to edge habitats not actively being managed during the study period, dense herbaceous vegetation resulted in a steep decline in some open habitat species. This was noticeable, *e.g.* for

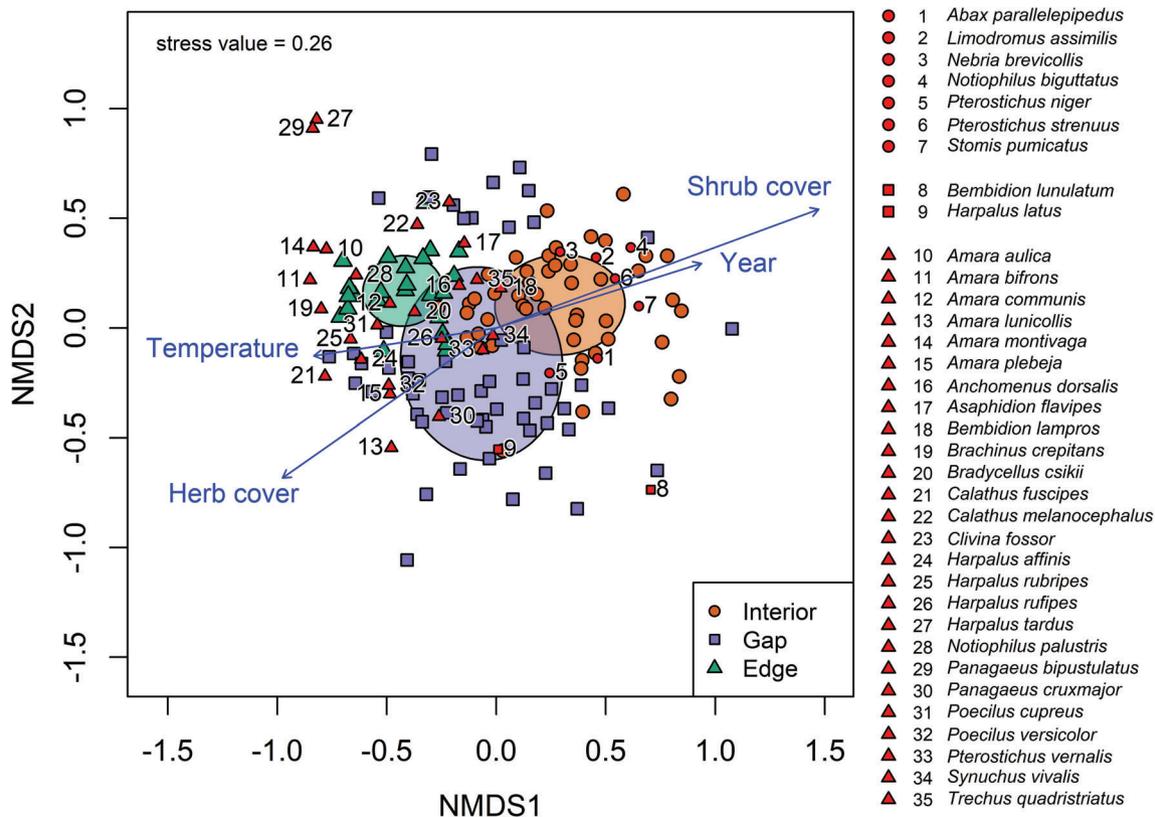


Figure 4 Nonmetric multidimensional scaling of carabid assemblages. Points show the 128 traps of all 3 years categorized in edge, gap and interior habitat types within short rotation coppices. Blue arrows indicate significant environmental effects ($P < 0.05$). Ellipses show standard deviation of habitat type. Indicator species according to multi-level pattern analysis (right-hand side list) are displayed in red with corresponding symbol of habitat type.

A. dorsalis, *B. crepitans*, *H. affinis* and *H. rufipes*, which declined steadily from 2013 to 2015 in edges. It can therefore be argued that lacking management of herbaceous layer (e.g. recurring removal), consequently leading to high and dense herbaceous vegetation, can have effects similar to canopy closure of SRCs for some open habitat species.

Interior habitat indicator species drastically increased in their dominance from edge to gap to interior habitat types. This was visible for interior indicators like *Abax parallelepipedus* (Piller & Mitterpracher, 1783), *Limnodromus assimilis* (Paykull, 1790) and *Nebria brevicollis* (Fabricius, 1792), and although less pronounced, we found similar trends for *Notiophilus biguttatus* (Fabricius, 1779), *Pterostichus strenuus* (Panzer, 1796) and *Stomis pumicatus* (Panzer, 1796). All seven indicator species for interiors are listed by Müller-Motzfeld (2001) as forest carabids, preferring or bound to forest habitats. Müller-Motzfeld (2001) identified 116 carabids in Germany as forest carabids, of which 20 were found in our study. Of those 20, 16 species were recorded in interiors, while 15 were recorded in gaps and 14 in edges. The dominance of sampled forest species decreased from interiors to gaps to edges. The most abundant forest carabids in our study were *P. niger* and *Carabus violaceus pupurascens* Fabricius, 1787, both decreasing in dominance from interiors to edges.

The moderate presence of interior indicators in gaps and edges can be attributed to dispersal between neighbouring habitats,

which has often been observed for carabids before (Koivula *et al.*, 2004; Roume *et al.*, 2011; Magura, 2017). Magura (2017) and Roume *et al.* (2011) found higher dispersal ability from forest species into open habitat than *vice versa*. However, permeability of forest edges by carabids is dependent on their history (Magura *et al.*, 2017; Magura & Lövei, 2020). Although edges created through anthropogenic influence are penetrable for open habitat species, they are avoided by forest species (Magura & Lövei, 2020). Therefore, dispersal of forest carabids from interiors into gaps and edges can be limited.

Our findings support results obtained by previous studies, suggesting that carabid species composition in SRCs shifts towards forest assemblages (Allegro & Sciaky, 2003), but also shows that shift in interiors is more pronounced than in gaps. Gaps could therefore retain open habitat species that could otherwise be lost in SRCs. Gaps were the only habitats where species density increased during the sampling period from 2013 to 2015. Increases in carabid diversity were also observed in early forest succession stages after clear-cuts (Buddle *et al.*, 2006; Magura *et al.*, 2015) and wildfires (Buddle *et al.*, 2006). Following disturbance, sites are quickly colonized by carabids with good dispersal abilities and generalist species (Magura *et al.*, 2015). Also, some forest species are able to survive harvest treatments and are likely to be trapped 1–2 years after clear cuts pitfall traps (Buddle *et al.*, 2006). The mixture of quickly invading

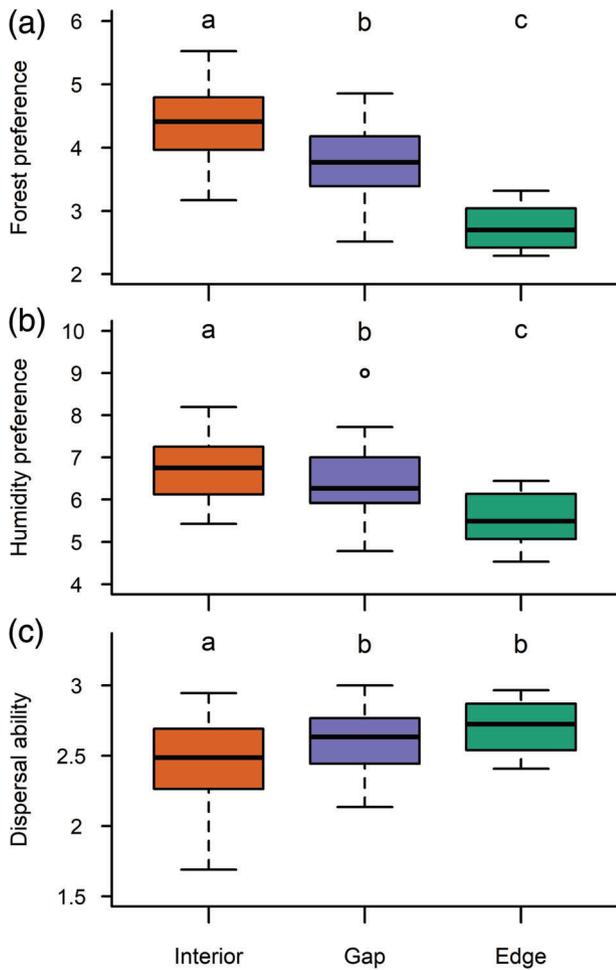


Figure 5 (a) Forest preference, (b) humidity preference and (c) dispersal ability of all different habitat types on trap level per year. For literature sources of traits see Table S1. Small letters indicate significant differences ($P < 0.05$) between habitat types, resulting from generalized mixed-effect models with habitat type as predictor.

open habitat species and remainder of some forest species can therefore lead to an increase in species density of carabids shortly after creating gaps. However, this effect could only be short-lived if the herb layer in gaps remains unmanaged after implementation and similar effects of open habitat species declines, as observed in edges, are likely.

Environmental drivers

Our findings suggest that the differences in species compositions between habitat types result from different structural features of habitats and their influences on prevailing microclimatic conditions. Carabids are affected by abiotic conditions such as soil moisture, air and soil temperatures and light availability (Thiele, 1977), which drastically change during a coppice cycle. After establishment or harvest of an SRC, the habitat and microclimatic conditions change rapidly through quick growth of young trees. With closing canopy, the light availability decreases,

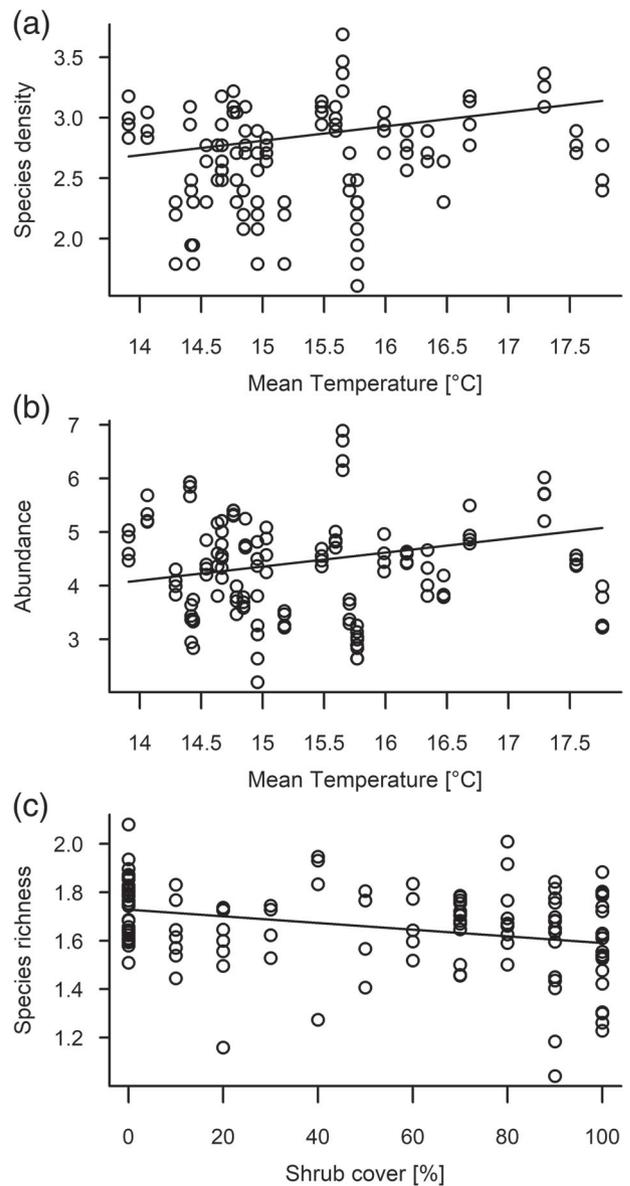


Figure 6 Regression plots of all significant effects from generalized mixed-effect models on trap level per year. All y-axes are log₁₀ transformed. (a, b) Effects of temperature on species density and abundance, (c) effects of shrub cover on species richness.

air and soil temperatures drop, and soil moisture evaporates slower due to less wind and lower temperatures (De Frenne *et al.*, 2019). The understory herb layer diversity decreases, favouring forest understory vegetation over grassland vegetation (Baum *et al.*, 2012; Birmele *et al.*, 2015).

Carabids are affected by the changes in the ground-level vegetation by multiple ways. Although structurally complex vegetation offers carabids microsites for oviposition and shelter, it also gives potential prey a better chance of escaping and therefore consequently affecting success of different hunting strategies (Brose, 2003; Rouabah *et al.*, 2015). However, habitat complexity had no significant effect on carabid catches in a study conducted by Esch *et al.* (2007).

Table 2 Results of generalized linear mixed-effects models for species density, abundance (Poisson errors) and species richness (Gaussian errors) with herb cover, shrub cover and temperature as predictor variables

Predictor variable	Species density				Abundance				Species richness			
	Estimate	SE	z-value	P-value	Estimate	SE	z-value	P-value	Estimate	SE	z-value	P-value
(Intercept)	1.02	0.86	1.19	0.236	0.45	1.42	0.31	0.754	3.24	1.84	1.76	0.079
Herb cover	-0.09	0.12	-0.77	0.443	-0.13	0.19	-0.69	0.487	-0.39	0.32	-1.25	0.211
Shrub cover	-0.10	0.12	-0.80	0.423	0.30	0.20	1.49	0.137	-0.61	0.29	-2.11	0.035
Temperature	0.12	0.05	2.20	0.028	0.26	0.09	3.01	0.003	0.18	0.11	1.54	0.123

Bold values indicate significance ($P < 0.05$).

In our study, herb layer had no direct effect on carabid species density, abundance or species richness, but was a significant vector affecting species compositions in nonmetric multidimensional scaling. Contrary to our study, the influence of presence and structure of herb layer on carabids has been proven in multiple studies before (Spence & Niemelä, 1994; Pakeman & Stockan, 2014).

The on going succession of shrub cover from 2013 to 2015 had a significant effect on species composition. During the three sampling years, shrub cover increased in interior habitats and the closing canopy allowed less light to penetrate, reducing temperatures on ground level. Temperature was inversely correlated with shrub cover but positively correlated with herb cover (Table S6). Thiele (1977) found that temperature and light have the greatest impact on carabids in open habitats. We also found significant positive effects of temperature on species density and abundance.

Species density and abundance increased with increasing temperature, whereas species richness declined with increasing shrub cover (Fig. 6). This led to a significantly higher carabid species density in edges around SRCs, than in interiors or gaps. The higher species density in edges could therefore be, at least partially, attributed to the overall higher abundance, induced by elevated activity levels of carabids in habitats with greater temperatures.

There are general differences between open habitats and habitats with canopy closure (temperature, humidity and ground vegetation), which can be used to explain the response of carabids. In general, open habitats host higher carabid diversity than e.g. forest interiors (Niemelä & Halme, 1992; Halme & Niemelä, 1993; Magura *et al.*, 2001; Koivula *et al.*, 2004; Roume *et al.*, 2011). The closed canopy of SRC might provide microclimatic conditions similar to forests. Therefore, a decline in species richness with increasing canopy closure is expected. Furthermore, according to the edge effect hypothesis, edges host higher species diversity than their adjacent areas (Odum & Barrett, 1971). That edge effects significantly affect carabids was revealed by multiple studies before (Magura *et al.*, 2001; Molnár *et al.*, 2001; Koivula *et al.*, 2004; Tóthmérész *et al.*, 2014).

Conclusions

Alpha diversity of carabids was higher in gaps than SRC interiors. Furthermore, gaps hosted significant different assemblages than interiors nearby. Hence, our results suggest that gap-implementation can support overall carabid diversity in SRC

due to higher species richness and less pronounced shifts in species composition towards forest species in gaps than interiors. Gaps can therefore host open habitat species that would otherwise decrease significantly in their dominance or might ultimately be lost in SRCs. These positive effects can be largely attributed to microclimate conditions. However, to uphold the positive effects of gap implementation on ground beetles, a recurring removal of herbaceous vegetation in gaps might be necessary. The cost-efficiency for such measures must be individually evaluated based on local context.

Acknowledgements

Peter Kriegel received funds from the Bauer- und Stemmler Stiftung. Fieldwork was initiated and financed by Naturschutzbund Deutschland e.V. We thank Vissmann and its representative Hans-Moritz von Harling for making the studied sites available for this research. The authors declare that they have no conflicts of interest. Open access funding enabled and organized by Projekt DEAL.

Authors' contributions

Michael-Andreas Fritze conducted fieldwork and determined carabids. Peter Kriegel did the analysis and wrote the paper with input from Simon Thorn and Michael-Andreas Fritze. All authors gave final approval for publication.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

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

Figure S1: Spline correlogram estimated from spatial data for a) species density, b) abundance and c) species richness.

Table S1: Overview of ecological traits of carabids and associated literature sources. Data taken from: Lindroth (1992), Marggi (1992) Homburg *et al.* (2014), Trautner (2017), Köhler *et al.* (2019) and are supplemented with expert knowledge.

Table S2: Species list with affiliated trait values. For explanation of trait values see Table S1.

Table S3: Cumulative contributions of most influential species calculated by similarity percentages between two habitat types.

Table S4: Results of permutational multivariate analysis for all pairwise combinations of habitat types. Column *p*.adj shows adjusted *p*-values with *Bonferroni* correction.

Table S5: Results of generalized linear mixed-effect models for forest preference, humidity preference and dispersal ability with herb cover, shrub, cover, temperature and habitat types as predictor variables. Bold values indicate significance ($p < 0.05$). Analysis carried out on trap level.

Table S6: Correlation matrix of predictor variables used in linear mixed-effect models.

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Accepted 21 March 2021

First published online 5 April 2021