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**The beetle in the forest: Equivocal effect of habitat alteration on
ground beetle assemblages, from the community level to the
individuals' perspective**



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1. Introduction - Losing the beetles beyond the (forest) tree

Forests as the major original landscape element in Europe

It is a feasible conclusion that there were more forests in Europe in the early Holocene than nowadays (Desender et al. 1999, Fyfe et al. 2015). The history of the woodland cover of the continent cannot be described as a linear process but more likely as periods of forest expansions and reductions (Desender et al. 1999). The transformation of the European landscape has been a long and complex process and also connected with the conversion of wild woodlands into a mosaic of pastures, forests and heathlands. In addition the habitat fragmentation have also become a major driver of land cover change in Western Europe (Figure 1.1). While this process may involve the above mentioned factors, the major long-term trend has been the transition from a nature-dominated to a more human-dominated state. The current composition of land cover in Europe is dominated by agricultural areas (representing 41.1% of the land, mostly designated as arable land, permanent crops and grassland), followed by forest (32.6%) and unused or abandoned land (15.8%), leaving the remaining land to urban and industrial areas and infrastructure. The main land cover change in recent decades identified a decrease in croplands, followed by an expansion of areas covered by pastures and forests (partly due to the decline in crop production), and an expansion in urban land (Garcia-Martin et al. 2021). These changes in land use were associated with the growth of human populations relying on agricultural activities, and their need for arable and grazing land, along with timber and other forest products (Fyfe et al. 2015) and also for space for living (McIntyre 2011).

Forests as natural capitals

Nowadays, the cover of the forests and other wooded lands (including plantations) is exceed 43.52% of the European Union's terrestrial land; however, the majority of the forests are strongly modified, and only 4% of those can be considered as undisturbed, where natural processes and structures are dominant (Sabatini et al. 2018, European Commission 2021). In primary forests, rare, coarse-scale disturbances such as windthrows or forest fires and frequent fine-scale disturbances in the form of spontaneous gap dynamics may support the structural heterogeneity either at stand- or at landscape level (Bengtsson et al. 2000). The progressive technical development in forestry and the recurrent disturbance caused by the production-oriented and the most common rotation forest management had increasing negative effects on biodiversity (Bengtsson et al. 2000, Vanbergen et al. 2005, Hermy & Verheyen 2007). European forests managed by rotation forestry systems are characterized by even-aged stands, low tree species richness, homogenous structure and low amount and heterogeneity of tree-related microhabitats microhabitats such as large dead logs or veteran

trees. However, many of these managed forests may preserve high biodiversity including thousands of forest specialist species as well as special habitat types (European Commission 2021).

In the last decades, new initiatives appeared in forest management that, besides providing timber production, also aim to sustain natural biochemical processes and biodiversity. Such goals are reached, for instance, by the maintenance of old-growth attributes (Bauhus et al. 2009), continuous cover forestry (Pommerening & Murphy 2004), retention forestry (Lindenmayer et al. 2012, Mori & Kitagawa 2014) and forest management mimicking natural disturbances (Bengtsson et al. 2000).

With these various approaches, it is crucial to explore how production-oriented forestry can be harmonized with initiatives where biodiversity conservation is a functional part of forest management.

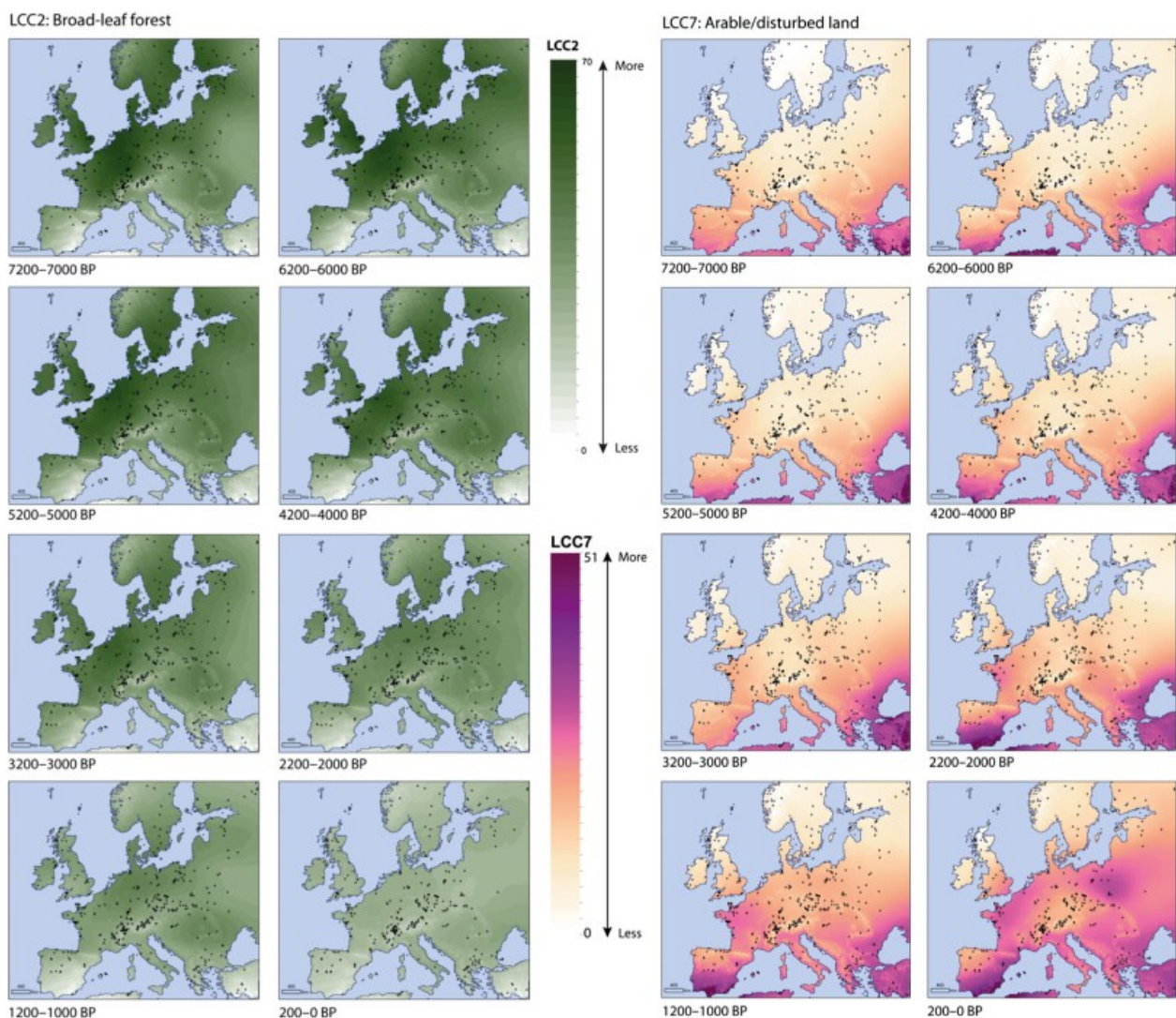


Figure 1.1 Land-use cover change (LCC) in Europe based on spatially interpolated pseudobiomization (PBM) for broad-leaf forest (LCC2) and for arable/disturbed land (LCC7). Black circles represent pollen site locations used for PBM. Figure modified after Fyfe et al. 2015.

Forests replaced by human settlements

Although the majority of forests are considered as natural capitals over centuries in Europe, we cannot ignore the fact that the increasing human population may demand more land for agriculture and also a vast amount of space for living (McIntyre 2011). Due to the economic development, the urban settlements, town, cities and megalopolises became the most common space for living worldwide. In the 20th century, urbanisation have become the fastest and most prominent driver of habitat alteration in the world (McIntyre 2011). Urban areas typically have high human density, energy concentration, altered biochemical cycles, pollution and only remnants of the original habitat elements/types (McIntyre et al. 2001). Europe has supported large human populations over centuries, and the original vegetation including semi-natural forests has been modified in many different ways. Furthermore the term semi-natural or managed natural forest defined as “*a stand which is composed predominantly of native trees and shrub species which have not been planted. Also, a forest which has developed gradually or accidentally, as its location or site quality was not suited for intensive exploitation or production-oriented management (e.g., in mountainous regions). This kind of reconstruction of the natural forest cover can be or has been achieved by using various silvicultural practices, e.g., natural regeneration or selective thinning and in some cases also planting*” (European Environmental Agency 2022). The extension of built-up areas reduces the size of semi-natural habitat patches such as forests and alters environmental conditions (Meyer et al. 2020a). Forests are one of the major semi-natural areas in urban landscapes. Furthermore, urban forests also deliver important ecosystem services including water retention, climate regulation, air filtering, carbon and nitrogen sequestration (Elmqvist et al. 2015, Meyer et al. 2020b). In the densely populated European countries, there are hardly any “natural” area left, thus it is crucial to explore how the intensive anthropogenic disturbance may affect the remaining network of semi-natural habitats. In order to sensibly manage the remaining biodiversity, there are calls for knowledge of ecosystem responses to the influence of urbanisation (McDonnell & Pickett 1990). Biodiversity is an important indicator of the functional state of ecosystems (Naeem et al. 1994) and contributes to the well-being of city dwellers. The effects of urbanisation on nature can be assessed by studying ecosystem structures and functions along urban-rural gradients (McDonnell & Pickett 1990).

Forest changes and carabids within

Various management practices can undoubtedly influence ecological processes as well as insect assemblages in forested habitats (Christensen & Emborg 1996, Paillet et al. 2018), even though the

conservation impacts of these changes remain a complex task to fully understand. Thus, it is crucial to explore the interactions between various habitat alterations and forest-dwelling organisms to unravel possible ecological consequences. Ground-dwelling predatory arthropods such as carabids (Coleoptera: Carabidae) are good indicators of the effects of various forest managements (Niemelä et al. 2007). This group has a relatively short generation time (Thiele 1977, Lövei & Sunderland 1996) and a relatively high position in the food web (Wootton 1998) allowing for a complex response to changes in their abiotic and biotic environment. Their assemblage composition is very sensitive to structural complexity of forest stands at different temporal and spatial scales (Niemelä et al. 2007, Negro et al. 2008). Within the framework of biodiversity and conservation studies, species composition, richness, alpha diversity indices and abundance are the simplest measures for biodiversity based on the taxonomic identity of the individuals (Magura 2017). Changes in the taxon-based measures for ground beetle assemblages will evidently reflect their functional role in forest ecosystems, because the functional traits are highly connected with their taxonomic identity (Magura 2017, Magura & Lövei 2019). The inclusion of species' functional traits often appears with the premise of exploring the resource utilization, dispersal, or reproduction. Schirmel et al. (2012) found that functional traits may contribute to trait-based environmental filtering in forming species communities. Although functional trait analysis can indirectly estimate the ecosystem functions, their use is more suitable at population-level (Murray et al. 2017). Nevertheless the community measures including functional traits are widely used; new facets appeared and serve as good proxies for ecosystem functioning including animal behaviour. However it is important to explore the spatio-temporal habitat use of beetles including other methods employed alongside of community measures by pitfall trapping such as individual movement by radio telemetry or taxon-specific predation pressure. These alternative methods as a proxy for animal behaviour contribute to understand the behavioural aspects of habitat utilisation for better prediction of species-specific responses to habitat alteration. All these clues mentioned above may also prompted us to explore the potential knowledge gaps in our understanding how animal behaviour can be generalized as a functional component of community-level measures.

1.1 Motivation and thesis structure with the publications used therein

This work consists of three major conceptual parts. *The 2nd chapter is about the urbanisation-driven habitat alterations in forested habitats in Denmark, which is a set of case studies that endeavour into the era when the major motivation was to explore whether the process of urbanisation harms the arthropod biodiversity in urban green habitats such as forests. In the 3rd chapter, the focus is on*

the fact how managed natural forests can be used as natural capitals. The question is how. One of the ample conflict between mankind and the natural environment is the constant human demand for natural resources. It is therefore important to strike for a good balance between the rational use of natural resources and the conservation of biodiversity in semi-natural habitats. This issue is also true for forest management, where the sustainable use of forests and woodlands for timber production is crucial for future generations. The presented case studies demonstrate how the different management practices of two forestry systems (rotation vs continuous cover forestry) can affect the various aspects of carabid assemblages and populations. These above-mentioned parts follow a common approach. Their focus is on testing hypotheses about the individuals' perspectives on organization of insect assemblages in forests. At the community level, there are several traits, which are well-known community descriptors such as species richness and composition, various diversity indices and functional diversity of morphological traits. However, at the individual/population level, there is a prompt feedback from the environmental stress and conditions through the behavioural response (developmental homeostasis and movement) which can be reflected in population dynamics. In addition, there is a conceptual knowledge gap between the two organizational levels: we do not yet know how the individuals' perspective can be associated with the assemblage descriptors. *Therefore in summary in the second and third chapters, I am going to introduce the relationships between animal behaviour and assemblage-level descriptors in the context of urbanisation and forest management. The 4th part shows the methodological advances, which have been invented or considered for future use in ecology.* These include statistical issues, graphical inventions and methodical corrections.

Although this synthesis work is based on research activities where I was a principal investigator, there are several colleagues who contributed to these projects significantly. These achievement are reflected in the language of this work serving as a sort of acknowledgment to their valuable contribution. In addition, I use the terms "assemblage" and "community" with different purposes. The first term will refer the observed beetles populations where I considered no interaction between individuals. I intend to use the term "community" for theoretical purposes, when I refer to conceptual models, proven facts by previous researches or textbook examples. The thesis is based on the following publications (impact factors (IF) corresponds to the year of publication) below. Although there are several additional publications available for these projects, these publications were directly used during the writing phase of this work. The thesis tends to be a synthesis rather than a direct summary of the following papers:

1. Elek Z, Růžičková J, Ódor P (2022): Functional plasticity of carabids can presume better the changes in community composition than taxon-based descriptors. *Ecological Applications*, 32(1): 1–13. <https://doi.org/10.1002/eap.2460> (IF:6.105)
2. Elek Z, Růžičková J, Ódor P (2021): Individual decisions drive the changes in movement patterns of ground beetles between forestry management types. *Biologia*, 76: 3287–3296. <https://doi.org/10.1007/s11756-021-00805-x> (IF:1.653)
3. Růžičková J, Elek Z (2021): Recording fine-scale movement of ground beetles by two methods: Potentials and methodological pitfalls. *Ecology and Evolution*, 11: 8562–8572. <https://doi.org/10.1002/ece3.7670> (IF:3.167)
4. Růžičková J, Elek Z (2021): Unequivocal Differences in Predation Pressure on Large Carabid Beetles between Forestry Treatments. *Diversity*, 13: 484. <https://doi.org/https://doi.org/10.3390/d13100484> (IF:3.029)
5. Růžičková J, Sándor B, Szálakvo A, 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(1): 77–86. <https://doi.org/10.17109/AZH.67.1.77.2021> (IF:0.97)
6. Lövei G L, Horváth R, Elek Z, Magura T (2019): Diversity and assemblage filtering in ground-dwelling spiders (Araneae) along an urbanisation gradient in Denmark. *Urban Ecosystems*, 22(2): 345–353. <https://doi.org/10.1007/s11252-018-0819-x> (IF:2.547)
7. Elek Z, Kovács B, Aszalós R, Boros G, Samu, F, Tinya F, Ódor P (2018): Taxon-specific responses to different forestry treatments in a temperate forest. *Scientific Reports*, 8(1): 16990. <https://doi.org/10.1038/s41598-018-35159-z> (IF:4.011)
8. Lövei G L, Elek Z, Howe A, Enggaard M (2018): The use of percentile-percentile plots to compare differences in seasonal dynamics, illustrated by the case of ground beetles (Coleoptera, Carabidae) reacting to urbanisation. *Community Ecology*, 19(1): 1–8. <https://doi.org/10.1556/168.2018.19.1.1> (IF:0.746)
9. Elek Z, Howe A G, Enggaard M K, Lövei G L (2017): Seasonal dynamics of common ground beetles (Coleoptera: Carabidae) along an urbanisation gradient near Sorø, Zealand, Denmark. *Entomologica Fennica*, 28: 27–40. (IF:0.943)
10. Elek Z, Lövei G L, Bártki M (2017): Sex-specific interaction of body condition and asymmetry in carabids in distinct urbanisation stages. *Community Ecology*, 18(3): 253–259. <https://doi.org/10.1556/168.2017.18.3.4> (IF:0.934)

11. Elek Z, Lövei G L, Bártki M (2014): No increase in fluctuating asymmetry in ground beetles (Carabidae) as urbanisation progresses. *Community Ecology*, 15(2): 131–138.
<https://doi.org/10.1556/C> (IF:1.214)
12. Elek Z, Dauffy-Richard E, Gosselin F (2010): Carabid species responses to hybrid poplar plantations in floodplains in France. *Forest Ecology and Management*, 260: 1446–1455.
<https://doi.org/10.1016/j.foreco.2010.07.034> (IF:1.992)
13. Elek Z, Lövei G L (2007): Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. *Acta Oecologica*, 32(1): 104–111.
<https://doi.org/10.1016/j.actao.2007.03.008> (IF:1.306)
14. Sapia M, Lövei G, Elek Z (2006): Effects of varying sampling effort on the observed diversity of carabid (Coleoptera : Carabidae) assemblages in the Danglebe Project, Denmark. *Entomologica Fennica*, 17(3): 345–350. (IF:0.25)

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2. Ground beetles of forest remnants in urbanised landscape

Urbanisation leads to modification of the original habitat (McIntyre et al. 2001). This change is often followed by the loss of the majority of its original plant and animal species (Marzluff et al. 2001) and accompanied by the replacement of native species by non-native ones (Kowarik 1995, Blair 1996, 2004). The biodiversity in urban forests provides important ecosystem services in cities, including the removal of dust, mitigation of microclimatic extremes, modulation of humidity (Bolund & Hunhammar 1999); however, the most significant ones probably are the psychological benefits resulting from human “biophilia” (Wilson 1984). An international research project, the “Globenet”, was initiated to conduct comparable studies in different countries to assess the influence of urbanisation on biodiversity (Niemelä et al. 2000). This project applied the forest-suburban-urban gradient approach (Pickett et al. 2001) using a common methodology (pitfall trapping) and evaluated the responses of a common invertebrate taxon (ground beetles, Carabidae) to urbanisation. In the Globenet project, three types of forested habitats (natural forest, suburban forested area and urban parks) were compared, representing different levels of disturbance described by the proportion of built-up area. Results from the Globenet Project on carabids have so far been published from Finland (Alaruikka et al. 2002, Venn et al. 2003), Canada (Niemelä et al. 2002), Bulgaria (Niemelä et al. 2002), Japan (Ishitani et al. 2003), Belgium (Gaublomme et al. 2005) and Hungary (Magura et al. 2004). These studies mostly found that carabid diversity was the highest in the least disturbed habitat, the original forest and species richness gradually decreased towards the most disturbed habitat, the urban park (Niemelä et al. 2002, Ishitani et al. 2003). A faunistic evaluation in Denmark however, indicated a different trend as the highest number of species was collected in the urban habitat, while the lowest one was found in the rural forest (Elek & Lövei 2005). Therefore it is crucial to identify the key components of ground beetle assemblages and populations that the most sensitively indicate the effects of urbanisation and thus can serve as indicators when looking for a sustainable management of urban green areas such as parks, private gardens, graveyards etc.

Methods commonly used in the urbanisation studies

Study area

The study area was in and around the town of Sorø (ca. 7000 inhabitants in 2003), a regional centre about 80 km west of Copenhagen, on the island of Zealand, Denmark. Three habitat types were selected according to the Globenet protocol: forest, suburban and urban areas (Fig. 2.1.1; Niemelä et al. 2000).

(1) The (semi- natural) *rural forest* was a large, near-continuous forest, ca. 3 km west from the town centre, bordered by Lake Sorø and the outskirts of the town. Four different forest patches were selected at least 1 km from each other and all were dominated by beech (*Fagus sylvatica*). Smaller groups of pine (*Pinus sylvestris*) and individuals of other deciduous tree species were also present but only near to the edges of forest roads. The forest blocks were managed by continuous-cover forestry system, but the understory was not thinned and the smaller branches of the felled trees were left on the ground. The seasonally dense herb layer – with springtime biomass maximum – contained *Anemone silvestris*, *A. ranunculoides*, and *Leucjum vernum* as dominant species of the spring aspect.

(2) The *suburban forest* was located north-east of the town centre and was surrounded by the old cemetery, an overgrown old ditch, a dirt road and a wet forest area under intensive forestry management. This area started approximately 1 km from the edge of the Sorø Akademi Park and extended to the forested area beyond the town. The built-up surface was approximately 20% and the understory indicated nitrogen-rich soil (e.g., high cover of nettle, *Urtica dioica*). In places, the undergrowth was a tangle of different weeds, a thick carpet of beech saplings, or thick litter layer. The dominant trees were beech and hornbeam (*Carpinus betulus*).

(3) The *urban park* was in the park complex of the Sorø Akademi. This large area had old forest patches with mainly beech, but also yew (*Taxus baccata*) and silver lime (*Tilia argentea*). In the dense shrub layer, hawthorn (*Crataegus monogyna*) and box (*Buxus sempervirens*) were common. The forest patches were separated by extensive, regularly mown grass areas. The park was “softly” managed: there were only gravel paths, and the mown grass, litter and cut branches were returned to the understory of the forested patches with barely scheduled management activities. A school and many visitors made the park complex the most disturbed habitat. The built-up area was about 40%. The park was isolated:

on one side, there is the Sorø Lake, on the other, the city centre. Traps were set only in the forest patches, and at least 5 m from an edge (Baker & Barmuta 2006). No more than 5 traps were set in one forest patch.

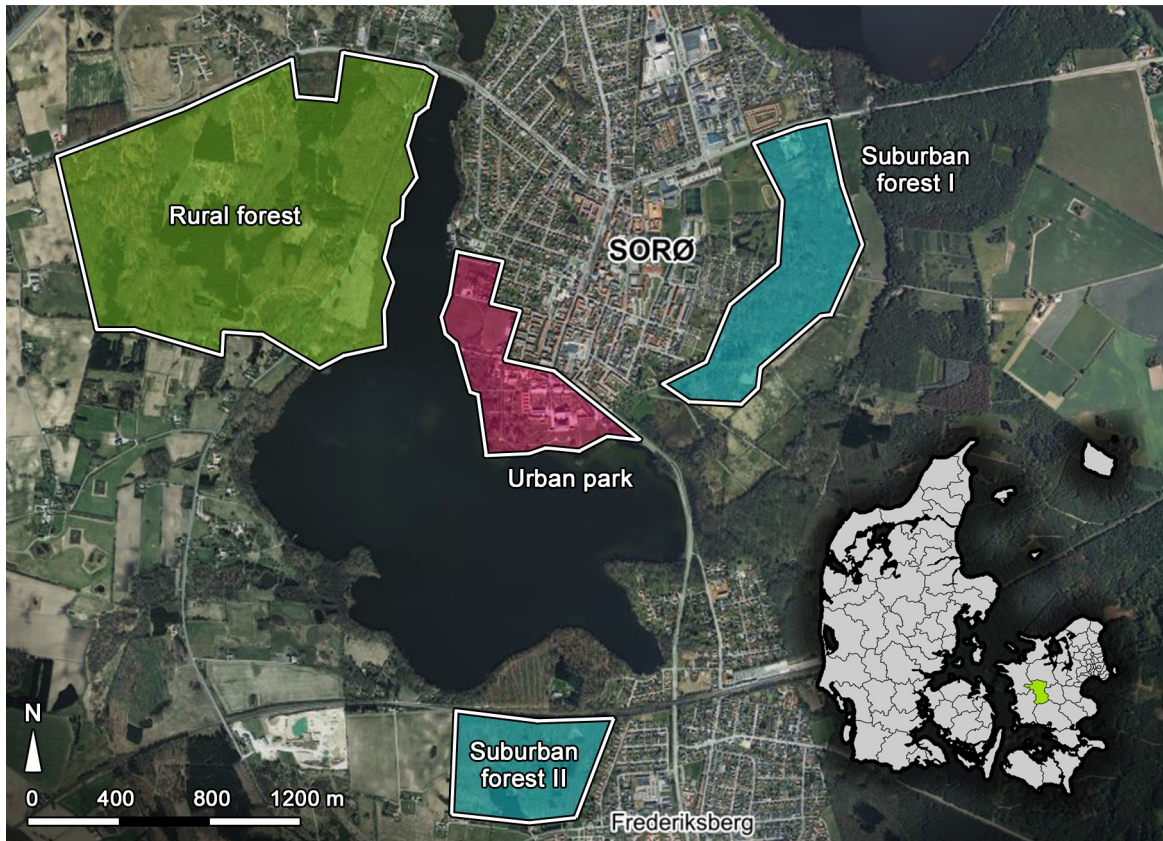


Fig. 2.1.1 Overview of the sampling sites in Sorø, Denmark. The contour lines designate the sampled forest areas, the suburban forest II was sampled only in 2005.

Sampling design

Carabid beetles were collected at each sampling areas using pitfall traps. Four spatial scales were used in trap deployment. Individual traps were placed at least 10 m apart at each site. Five traps formed a sub-group, separated by at least 20 m from the nearest sub-group and two such sub-groups (10 traps) formed a site. Four sites, at least 200 m from each other, were selected within each sampling area. This resulted a total of 120 traps along the forest-suburban-urban gradient (3 areas \times 4 sites \times 10 traps). In the park, we only had traps in forest patches that were at least 10 m in diameter, and preferably had beech trees. The minimum inter-trap distance was maintained, but due to patch configuration, it was not possible to deploy five traps in every forest patches. In cases

where less than five traps could be deployed due to the spatial constraints, the inter-patch distances were smaller than the distance to the neighbouring site.

Traps consisted of 70 mm diameter plastic cups, sunk into the ground with their rim level at the soil surface. Each trap contained about 200 ml of 70% ethylene glycol as a killing and preservative solution and a drop of odourless detergent to reduce surface tension. The individual traps were covered by galvanized metal plate (20 cm × 20 cm) to protect the trap contents from litter, rain, by-catch of and disturbance by small mammals and birds. Traps were checked fortnightly between late April and mid-October, 2004. The total trapping effort was 2,640 trap-weeks (120 traps × 22 weeks); only very few (< 10) trap catches were lost. In order to examine the impact of reduced sampling effort we operated the traps every second fortnight in 2005 (Sapia et al. 2006) resulting in a total sampling effort of 1,440 trap-weeks (120 traps × 12 weeks). In 2005, the suburban forest II was sampled in addition to the suburban forest I, because the size of the suburban forest I was reduced due to logging. The species composition was highly similar in these suburban areas based on non-metric multidimensional scaling (Elek & Lövei 2007).

The beetles were identified to species using keys by Lindroth (1985, 1986) and Hürka (1996). Voucher specimens were deposited in the Coleoptera Collection of the Zoological Museum, University of Copenhagen, Denmark. The term activity density was used for the number of individuals caught by the pitfall traps. The term refers to the empirical fact that catches of pitfall traps depend on the individuals' activity; the higher activity of the individuals, the more catches in the traps. The dataset collected in 2004 was used for assemblage composition studies (Chapter 2.1), whilst the two-year dataset were used for studies on seasonal dynamics (Chapter 2.2), developmental instability (Chapter 2.3) including fluctuating asymmetry (Chapter 2.3.1) and physiological condition (Chapter 2.3.2) and also in the Chapter 4.1 as graphical innovation.

2.1 Patterns in ground beetle assemblages along an urbanisation gradient

There are many facets of environmental change that can be linked to the advancing urbanisation. In these habitats, ground beetle assemblages undergo a substantial rearrangement indicating a general decrease in the carrying capacity of the urbanised habitats. By the evaluation criteria so far applied in published Globenet studies (species presence, total activity density over the season), generalist or ubiquitous species did not show significant trends in response to increasing disturbance as a result of urbanisation. However, species reactions are different: certain forest specialist species become rare or disappear, while other species only appear at the most urbanised habitats (Magura et al. 2010b). These controversies in the responses of carabid assemblages were therefore further explored with a focus on different disturbance hypotheses.

- Intermediate Disturbance Hypothesis:

The first and most widely known hypothesis concerning the effect of disturbance is the *Intermediate Disturbance Hypothesis* (IDH, Connell 1978). This hypothesis generally predicts the highest level of diversity at intermediate levels of disturbance.

- Increasing Disturbance Hypothesis:

As an alternative of IDH, the *Increasing Disturbance Hypothesis* (IDH2, Gray 1987, 1989) suggests that species richness should monotonously decrease with increasing level of disturbance.

- Habitat Specialist Hypothesis:

An increasing disturbance regime by urbanisation is predicted to cause a decrease in both abundance and species richness of forest specialists along the urbanisation gradient; i.e., *Habitat Specialist Hypothesis* (HSH, Magura et al. 2004).

- Opportunistic Species Hypothesis:

Gray (1989) hypothesized that in habitats influenced by disturbance, overall diversity should decrease and opportunistic (generalist) species should gain dominance (*Opportunistic Species Hypothesis*, OSH).

- Decreasing Mean Body Size Hypothesis:

Gray (1989) also suggested that in habitats affected by increased disturbance, the mean size of the species present should decrease (*Decreasing Mean Body Size Hypothesis*, DMB).

- Food-access Hypothesis:

The *Food-access Hypothesis* (FAH) suggests that the availability of food can be the most variable in the urban park due to its high environmental heterogeneity. The difference in habitat

heterogeneity among different patches of such an area is arguably smaller in forest habitats than in park habitats due to lower beta diversity. However, carabids can spend the majority of their life span within a radius of 5 m (Thiele 1977) which is especially true for their larvae. This creates the most favourable feeding conditions for omnivorous species, thus the number of omnivorous species is supposed to be the highest in the park.

Methods

Data analysis

For numerical analyses, beetles were classified according to their habitat preference, feeding type and body size. Habitat preference classes were forest specialists, open-habitat species and generalists, based on information in Lindroth (1985, 1986). Feeding preferences, based on literature information (Laroche 1990) included the classes of predators, omnivores and herbivores. To classify body size, data from Lindroth (1985, 1986) were used to calculate geometric means, and three classes (small: < 9.5 mm, medium: 9.6–15.1 mm and large: > 15.2 mm) were established using a size distribution graph. To test for differences in the overall carabid activity density and species richness among three sampling areas (forest, suburban and urban) and among the 12 sites, nested analyses of variance (ANOVAs) were performed using data from the individual traps (sites nested within the sampling areas). The abundance and species richness of the three habitat preference groups were also tested by nested ANOVA. Normality was tested by the Kolmogorov-Smirnov tests (Sokal & Rohlf 1995). When ANOVA revealed a significant difference among the means, Fisher's least significant difference test (LSD) for multiple comparisons was performed. The multidimensional scaling was applied to display similarities in the abundance of carabids among the sites using the Sørensen index of similarity.

Results

Assemblage characteristics

Overall 10,314 individuals belonging to 43 species were collected in 2004. The most abundant species were usually present at all three habitat types, although in unequal numbers. *Abax ater* Villers, 1789 was typical and the most abundant species in the suburban and rural forest area. *Pterostichus melanarius* (Illiger, 1783) occurred in all habitats, but it was most abundant in the

urban and rural forest areas. *Nebria brevicollis* (F., 1792) also occurred in all habitats, with the highest number of individuals in the urban park. *Agonum assimile* (Paykull, 1790) also present in all habitats, was dominant at the urban park. The only species present at all three habitat types but with the highest numbers in the suburban forest was *Carabus coriaceus* L., 1758. The Shannon diversity, being sensitive to the proportion of the rare species suggested that diversity was higher in the rural forest (1.95) than in either the suburban forest (1.69) or the urban park (1.67). The Berger-Parker dominance index, which puts more weight on evenness (Magurran 2004) was highest in the rural forest (0.53), compared to the suburban one (0.37) and urban park (0.4).

Patterns of activity density and species richness

The total number of individuals was significantly higher in the urban park (i.e., park) and rural forest than in the suburban one (Table 2.1.1). The number of individuals belonging to predatory (carnivorous) species was also significantly higher at the urban park and rural forest than at the suburban forest, while the abundance of generalists in the urban park was significantly higher than at the other ones. The number of forest species was high in the rural forest but in the suburban one and urban park, it did not differ significantly (Table 2.1.1). The number of open-habitat species in the urban park was significantly higher than at either the suburban forest or the rural one, but the latter two did not differ significantly. The species richness of carnivorous carabids was significantly higher in the rural forest than in the other two. In contrast, the number of omnivorous species was significantly higher in the urban park than at the suburban or rural forest areas, the last two not differing significantly from each other. There were more generalist species in both the urban park and rural forest than in the suburban one, but the first two did not differ significantly (Table 2.1.1).

Table 2.1.1 Results of nested ANOVAs indicating differences in carabid activity density and species richness of overall catches, feeding type and habitat affinity along the forest (F) - suburban (S) - urban (U) gradient. The last column shows the differences based on the LSD (least significant difference) test ($p < 0.05$). Significant variables/effects/results are marked by bold.

Characteristics		Source of variation	d.f.	MS	F	p	LSD test
<i>Activity density</i>	All species	Gradient	2	58721.43	14.66	< 0.001	U=F>S
		Sites	9	4004.38	0.94	0.48	
		Error	108	4217.66			
	Predators	Gradient	2	57364.31	15.05	< 0.05	U=F>S
		Sites	9	3810.76	0.91	0.51	
		Error	108	4171.93			
	Omnivores	Gradient	2	14.35	2.21	< 0.25	
		Sites	9	6.48	7.15	0.00	
		Error	108	0.90			
	Forest species	Gradient	2	24411.73	7.72	< 0.25	
		Sites	9	3161.33	2.10	0.03	
		Error	108	1499.48			
	Open-habitat species	Gradient	2	677.27	1.51	< 0.25	
		Sites	9	447.69	6.93	0.00	
		Error	108	64.58			
	Generalists	Gradient	2	20893.96	12.73	< 0.005	U>F>S
		Sites	9	1640.95	1.59	0.12	
		Error	108	1029.15			
<i>Species richness</i>	Total number of species	Gradient	2	114.43	3.85	ns	
		Sites	9	29.64	6.10	0.00	
		Error	108	4.86			
	Predators	Gradient	2	96.63	5.45	< 0.025	F>U>S
		Sites	9	17.70	5.00	0.00	
		Error	108	3.53			
	Omnivores	Gradient	2	5.85	4.33	< 0.05	U>S=F
		Sites	9	1.358	4.06	0.00	
		Error	108	0.33			
	Forest species	Gradient	2	70.05	11.99	< 0.001	F>U=S
		Sites	9	5.83	4.26	0.00	
		Error	108	1.37			
	Open-habitat species	Gradient	2	35.30	3.94	< 0.05	U>S=F
		Sites	9	8.94	8.77	0.00	
		Error	108	1.01			
	Generalist species	Gradient	2	23.63	6.79	< 0.01	U=F>S
		Sites	9	3.47	4.00	0.00	
		Error	108	0.86			

Size trends along the gradient

The activity density of small species did not differ significantly among the areas (Table 2.1.2) while that of medium-sized species was significantly higher in the urban park than in the suburban or in the rural forest areas (these two did not differ significantly). The activity density of large beetles was significantly higher in the suburban and rural forest areas than at the urban park. Large beetles were equally active at the rural and suburban forests (Table 2.1.2).

Table 2.1.2 Results of nested ANOVAs indicating differences in carabid activity density and species richness of body size trends along the forest (F) suburban (S) - urban (U) gradient. The last column shows the differences based on the LSD (least significant difference) test ($p < 0.05$). Significance is marked by bold.

Body size classes	Source of variation	d.f.	MS	F	<i>p</i>	LSD test
<i>Activity density</i>						
Small (< 9.5 mm)	Gradient	2	1116.52	1.89	n.s.	
	Sites	9	588.45	8.04	0.00	
	Error	108	588.45			
Medium (9.6-15.1 mm)	Gradient	2	23215.06	15.72	< 0.01	U>S=F
	Sites	9	1476.66	1.41	0.19	
	Error	108	1045.62			
Large (> 15.2 mm)	Gradient	2	42133.11	22.91	< 0.001	U<S=F
	Sites	9	1838.76	1.26	0.26	
	Error	108	1458.24			
<i>Species richness</i>						
Small (< 9.5 mm)	Gradient	2	69.77	6.00	< 0.01	U>S=F
	Sites	9	11.61	7.14	0.00	
	Error	108	1.62			
Medium (9.6-15.1 mm)	Gradient	2	26.27	5.26	< 0.025	U>F>S
	Sites	9	4.98	6.52	0.00	
	Error	108	0.76			
Large (> 15.2 mm)	Gradient	2	42133.11	22.91	< 0.001	U<S<F
	Sites	9	1838.76	1.26	0.04	
	Error	108	1458.28			

The species richness of small species was higher in the urban park, and showed significant difference in comparison to both other urbanisation stages, while the suburban and rural forest areas did not differ from each other (Fig. 2.1.2). The number of medium-sized species was highest in urban park, the rural forest had an intermediate position, and the least number of species was found in the suburban forest. The number of large ground beetles had the opposite pattern, the number of these species was highest in the rural forest area, the suburban one had an intermediate position, and the urban park were the least species-rich (Fig. 2.1.2).

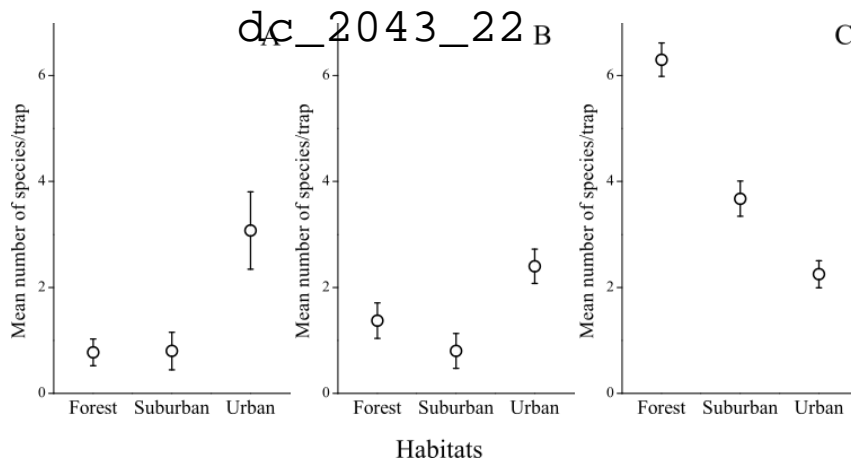


Figure 2.1.2 Species richness of small (body length < 9.5 mm) (A), medium-sized (9.6–15.1 mm) (B) and large (> 15.2 mm) (C) carabid species along the forest-suburban-urban gradient. The empty circles represent means, intervals indicate \pm S.E.M.

Comparison of different stages of urbanisation gradient

The results of non-metric multidimensional scaling with the Sørensen similarity plot showed a clear separation of areas along the forest-suburban-urban gradient. The points representing the rural forest and urban park traps separated well along the first axis, while the points representing the suburban and rural forest areas separated along the second axis (Fig. 2.1.3).

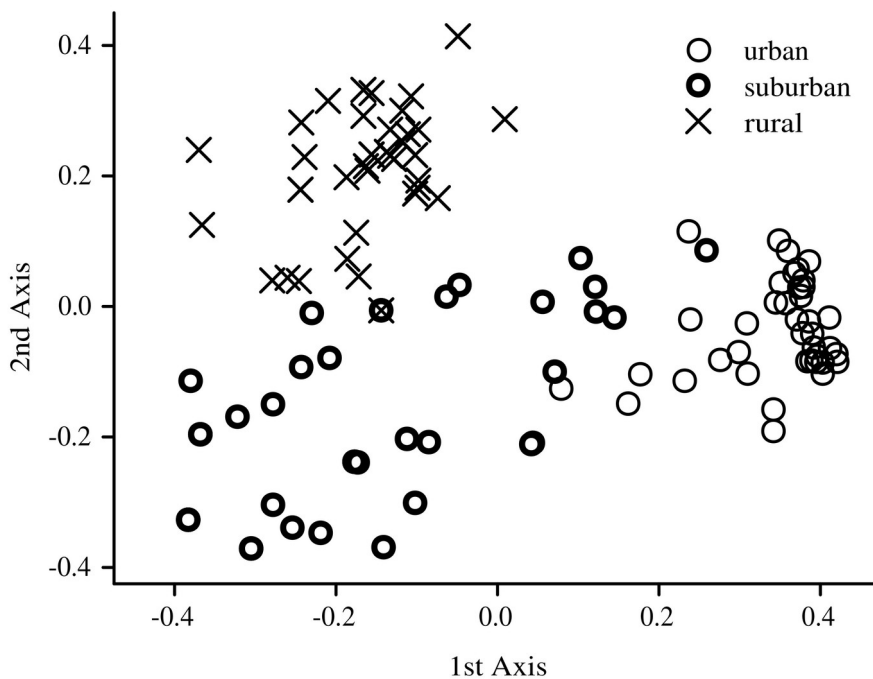


Figure 2.1.3 Graphical representation of the non-metric multidimensional scaling based on the total seasonal abundance of carabids captured, along a forest-suburban-urban gradient, using a plot of Sørensen similarity index. The stress of the two-dimensional configuration was 0.423.

Discussion

Patterns of species richness and activity density

Urbanisation causes several forms of disturbance, such as alteration, fragmentation and isolation of indigenous habitats, changes in temperature, moisture and edaphic conditions, and also pollution (Niemelä 1999). In spite of the urbanisation-induced environmental changes, the overall carabid diversity did not decrease in the disturbed habitats in this study. This deviates from trends found in several other studies including Finland, Bulgaria, Canada (Niemelä et al. 2002, but see Alaruikka et al. 2002 for Finland) and Japan (Ishitani et al. 2003). The overall species richness in Denmark (43 species) was intermediate in comparison to the findings of other Globenet studies. Considering the comparison of overall activity density, Denmark was the third most prolific site after Canada (Niemelä et al. 2002) and Belgium (Gaublomme et al. 2005). The similar latitudinal position of these Globenet sites could be the reason of this similarity. Our results were similar to the Hungarian Globenet case study (Magura et al. 2004), because in both countries the urban areas had the highest number of species. In both countries, there was a lake shore close to the urban park that might have provided additional habitats for carabids.

Intermediate disturbance is not the driver of beetles' diversity

The urbanisation induces several facets of the disturbance due to the increasing human density and impact of urban green areas. In addition, the increasing ratio of built-in areas and extension of air, soil and water pollution have impact on ecosystem processes (Bogyó et al. 2015). The tested hypotheses mentioned previously were supported except for intermediate disturbance ones. The findings of this study concurred with the results by Niemelä et al. (2002) and Magura et al. (2004) in not supporting the *IDH*: species richness was not the highest in the moderately disturbed suburban areas. This might be, because basal species in food webs probably conformed to this hypothesis, but top consumers did not (Wootton 1998). Carabids are considered as higher-level consumers (Lövei & Sunderland 1996). The results of this study supported the *OSH* prediction as the ratio of the individuals of the opportunistic carabid species to the total number of individuals was significantly higher in the urban area than in the other ones. Niemelä et al. (2002) reported similar findings concerning the dominance of opportunistic species in the urban areas of Canada and Finland. The results supported the *HSH*: both the number of forest species and their relative

frequency significantly increased from the urban park to the rural forest habitats. Also, the number of open-habitat species was significantly higher in the urban park than in the suburban and rural forests. A possible reason for this could be the impact of the surrounding habitat matrix: the presence of extensive open habitats (grassy areas) in the urban area. The matrix species had an impact on species richness patterns in forest fragments (Lövei et al. 2006, 2019). Other impacts of masking habitat fragmentation and disturbance effects included microclimatic changes at edges, short-term crowding effects and time lags (Ewers & Didham 2006). Previous studies (Thiele 1977, Magura et al. 2004) also emphasized that the number of open-habitat species increases as the closure of the forest stand decreases. In addition, the smaller species were more abundant in urban remnants of the original forest. The larger, less mobile species were more abundant in the rural forest area. However, the smaller forest species were also more abundant in urban remnants while the small- and medium-sized species were numerous in the urban park (*DMB* supported). Šustek (1987) analysing changes in the body size structure of carabids along an urbanisation gradient in Slovakia, also found that disturbance caused by urbanisation produced smaller average carabid body size. Carabids' body size varied from small in urban to larger in both suburban and forest areas in Bulgaria and Finland (Niemelä et al. 2002). This phenomenon, however, could be better understood by studying the possible size trends of species that occur in more than one habitat, because conditions experienced during larval development period often restrict adult body size. The *FAH* was supported because the species richness of omnivorous species was highest in the urban park. The predatory species were not absent from the park, indicating that park management was important to retain species from the original habitat, but as more predatory species were present in the forest habitats, conditions were obviously better there than in the park.

Implications for management

Forest fragments in an urbanised area can retain several species from the original forest fauna; however, the abundance and species richness of the stenotopic specialist species decrease with the increasing level of anthropogenic disturbance. The fragmentation of the original forest and the increasing level of human impact can lead to the loss of several forest species as well as to the successful colonization by generalist and open-habitat species, contribute to a relatively high number of species. Urban green areas, including forest patches, contribute to the quality of urban life and thus should be conserved. Apart from their recreational value, which is widely appreciated and enjoyed by human inhabitants, such green urban spaces provide seemingly adequate habitat for numerous species of ground beetles found in less developed forest areas some distance from the city

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core. Benign management, including gravel paths instead of asphalt, retaining as much plant material as possible within the habitat, and providing decaying wood in the understory increase habitat quality for invertebrates, contributing to their continued survival.

2.2 Seasonal dynamics of common ground beetles along an urbanisation gradient

Ground beetles are a species-rich family of Coleoptera, forming a significant part of the fauna active on the ground surface within most of their area of distribution (Lövei & Sunderland 1996). A total of 136 carabid species are known from Denmark (Lindroth 1985, 1986), but their population dynamics and life histories are not well documented. The pioneering studies by Schjøtz-Christensen (1965, 1968) clarified basic aspects of selected species in a heath area on Jutland, including reproductive activity and life span. Based on studies in NW Europe, Gyldenkaerne and Ravn (1998) presented a qualitative graphical summary of the seasonal activity of the most common species in agricultural landscape. More recent studies on ground beetles focus on the fauna of agricultural land (Lövei et al. 2002, 2005, Lövei & Magura 2017) and urban habitats (Elek & Lövei 2005, 2007). However, there remains a scarcity of published quantitative life-history studies on the native Danish ground beetle fauna (Jørum 1976a, 1980). Quantitative descriptive methods for seasonal activity are available (e.g., Fazekas et al. 1997) and climate change-related concerns make it relevant to have a more precise understanding of the spatial and temporal variation in the seasonal dynamics of species including ground beetles.

Therefore, the purpose of this chapter is to describe the seasonal dynamics in a standardised way (Fazekas et al. 1997) of the most common carabid species from Sorø, West Zealand, Denmark. “Heat island” effect of cities (McDonnell & Hahs 2015) was tested on the selected common species whether their spring activity would start earlier than in their original forest habitat.

Methods

Seasonal activity

Seasonal activity was described by the “quartile method” according to Fazekas et al. (1997). Captures (total number of individuals per fortnight) were first converted to cumulative values. To mitigate the impact of time-specific weather anomalies, the unweighted running means of three weeks were calculated the following way:

$$\bar{x}_a = (x_{a-1} + x_a + x_{a+1})/3$$

where x_{a-1} is the number of captures during the week before, and x_{a+1} is the same for the week following the central one, whose capture is x_a .

This running mean was used to calculate cumulative capture data, and the major dates (hereafter cardinal dates) of the seasonal activity were established. The three cardinal dates of the activity curve were the start, peak and end of the main activity period. The date of peak activity was the date when the cumulative number of individuals caught reached 50% of the total numbers collected. The beginning and the end of the main activity period were defined as the dates when 25% and 75% of the total number of individuals were captured, respectively. The early activity period extended from the start of the activity to the beginning of the main activity period, and the late activity period was defined as the period after the end of the main activity period until the activity had ceased. Only the activity of species with at least 10 individuals/site \times year was considered, in the case of unimodal activity profile. Although six species fulfilled the above mentioned criteria: *Abax ater* (Fabricius), *Carabus coriaceus* (L.), *C. nemoralis* (Müller), *C. hortensis* (L.) *Nebria brevicollis* and *Pterostichus melanarius* (Illiger); only the results for *C. nemoralis*, and *A. ater* are presented below in detail to portray the two major conceptual types of the responses and to keep the length of this chapter within reasonable limits. The response of the other selected species are mentioned in the discussion.

Results

Total seasonal activity

The total catch was 10,314 individuals belonging to 43 species in 2004, and 4,961 individuals of 38 species in 2005 (Elek & Lövei 2005). In general, ground beetle activity in 2005 was lower than in 2004, except in the suburban forests (Fig. 2.2.1). The total numbers captured were the highest in the urban park in both years (4,424 and 1,936 individuals in 2004 and 2005, respectively).

In the rural forest, ground beetle activity was strongly unimodal in both years, with high activity in mid- to late August (Fig. 2.2.1). The autumn activity in the rural forest was higher than in the urban park (Fig. 2.2.1). The activity density was the lowest in the suburban forests (2004: 1,591 individuals; 2005: 1,274 individuals), and showed a slight increase late in the season in both years, more in 2005 (Fig. 2.2.1). In the urban park, ground beetles showed bimodal activity with activity density peaks in late June and mid- August in 2004 (Fig. 2.2.1). This pattern was not easily visible in 2005 when the activity density levels were generally lower (Fig. 2.2.1).

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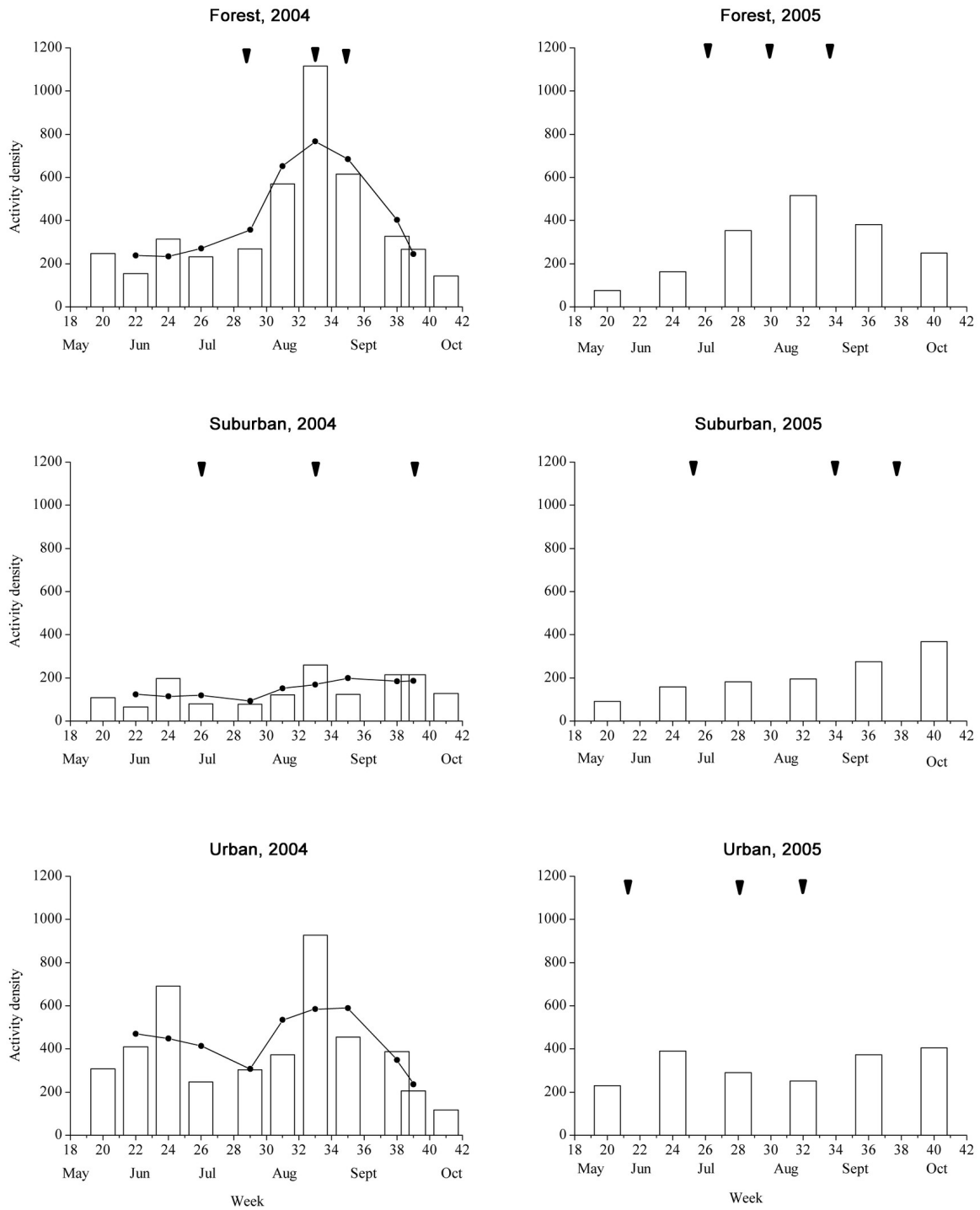


Figure 2.2.1 Seasonal dynamics of ground beetles in forested, suburban and urbanised habitats. Black arrows indicate the start, the peak and the end of the main activity periods, respectively. Bars indicate activity density (no. of individuals/trap \times fortnight) from start to end of sampling. Lines on the 2004 panels indicates running means of three weeks (and thus starts on 2nd sampling occasion and ends earlier than sampling did). Running means were not calculated for 2005, due to few sampling occasions.

Carabus nemoralis L, 1758

The seasonal activity of *C. nemoralis* was bimodal or slightly bimodal in all sites and years (Fig. 2.2.2). In five of the six site-year combinations studied, the spring activity density was higher than the autumn one; the only exception was in the suburban forests in 2005 (Fig. 2.2.2). This species likely remained active in the autumn longer than the trapping period. At the rural forest, this species showed slight bimodality with decreasing activity towards the end of the season in 2004. The spring activity peaked in early July, but the autumn peak was not clearly identifiable. The autumn activity peak in 2005 was almost missing (Fig. 2.2.2). In the suburban forests the species thrived: the activity density of this species was the highest in this habitat in both years, with an early high activity in week 24 and equally high activity in week 39 in 2004. The urban park was characterised by strong early activity, occurring about 4 weeks earlier than elsewhere (Fig. 2.2.2). It was also possible that this species became active before the start of the trapping. The second activity period was a little lower in 2004, again starting earlier in the urban park than elsewhere.

Abax ater (Villers)

This species occurred in the rural forest and suburban one in both years, but only in 2005 in the urban park (Fig. 2.2.3). In the rural forest, the activity was sharply unimodal with the main activity period falling between weeks 26-34 with an activity peak on week 33. The activity pattern between habitat types was similar in 2005. In the suburban forest, the main activity period occurred two and three weeks earlier in 2004 and 2005, respectively, than those in the rural one (Fig. 2.2.3). In 2004, the activity densities were much higher than in 2005 (Fig. 2.2.3).

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Carabus nemoralis

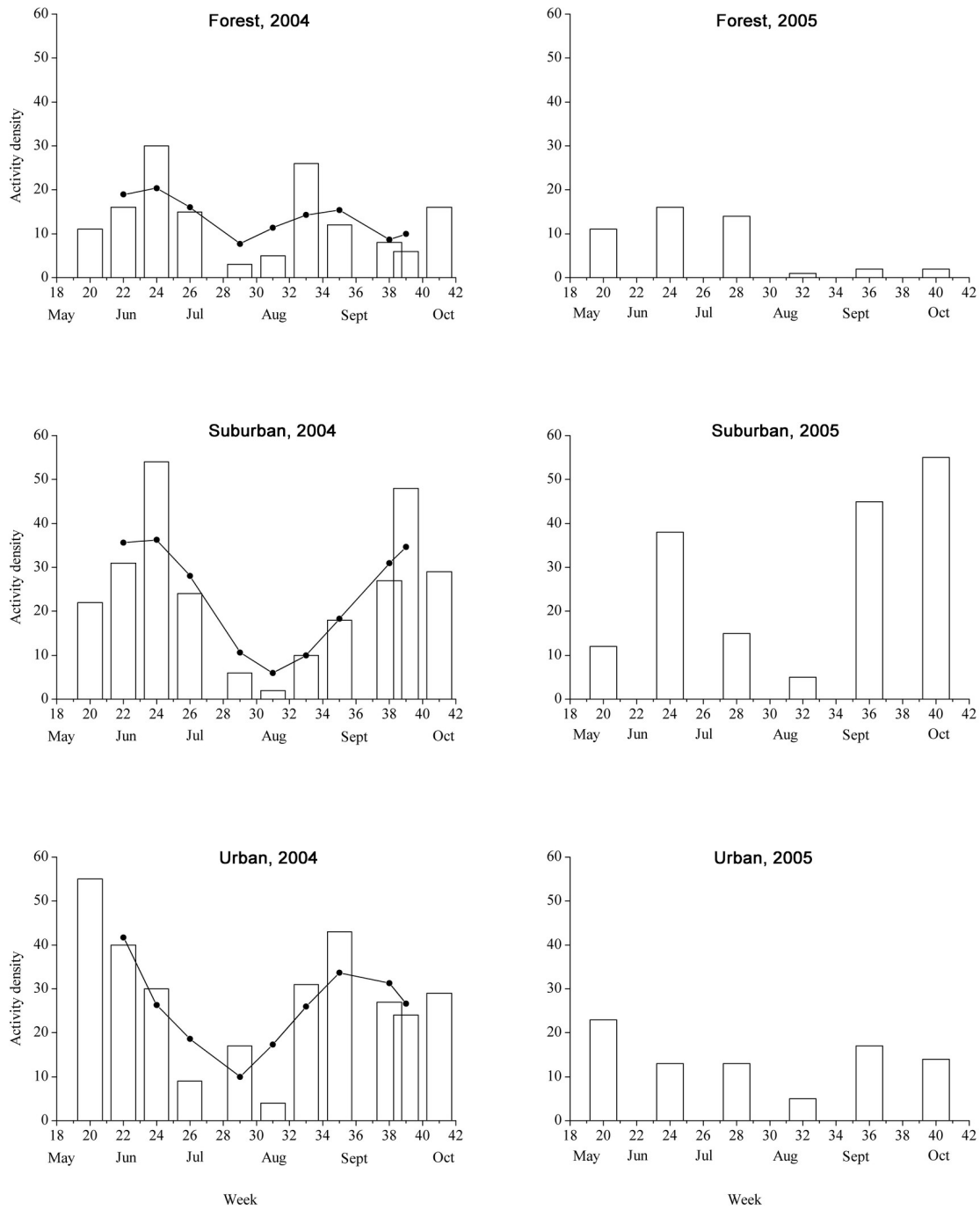


Figure 2.2.2 Seasonal dynamics of *Carabus nemoralis* at the three urbanisation stages (original forest, suburban and urban forest remnants). Black arrows indicate the start, the peak and the end of the main activity periods, respectively. Bars indicate activity density (no. of individuals/trap \times fortnight) from start to end of sampling. Lines on the 2004 panels indicates running means of three weeks (and thus starts on 2nd sampling occasion and ends earlier than sampling did). Running means were not calculated for 2005, due to the few sampling occasions.

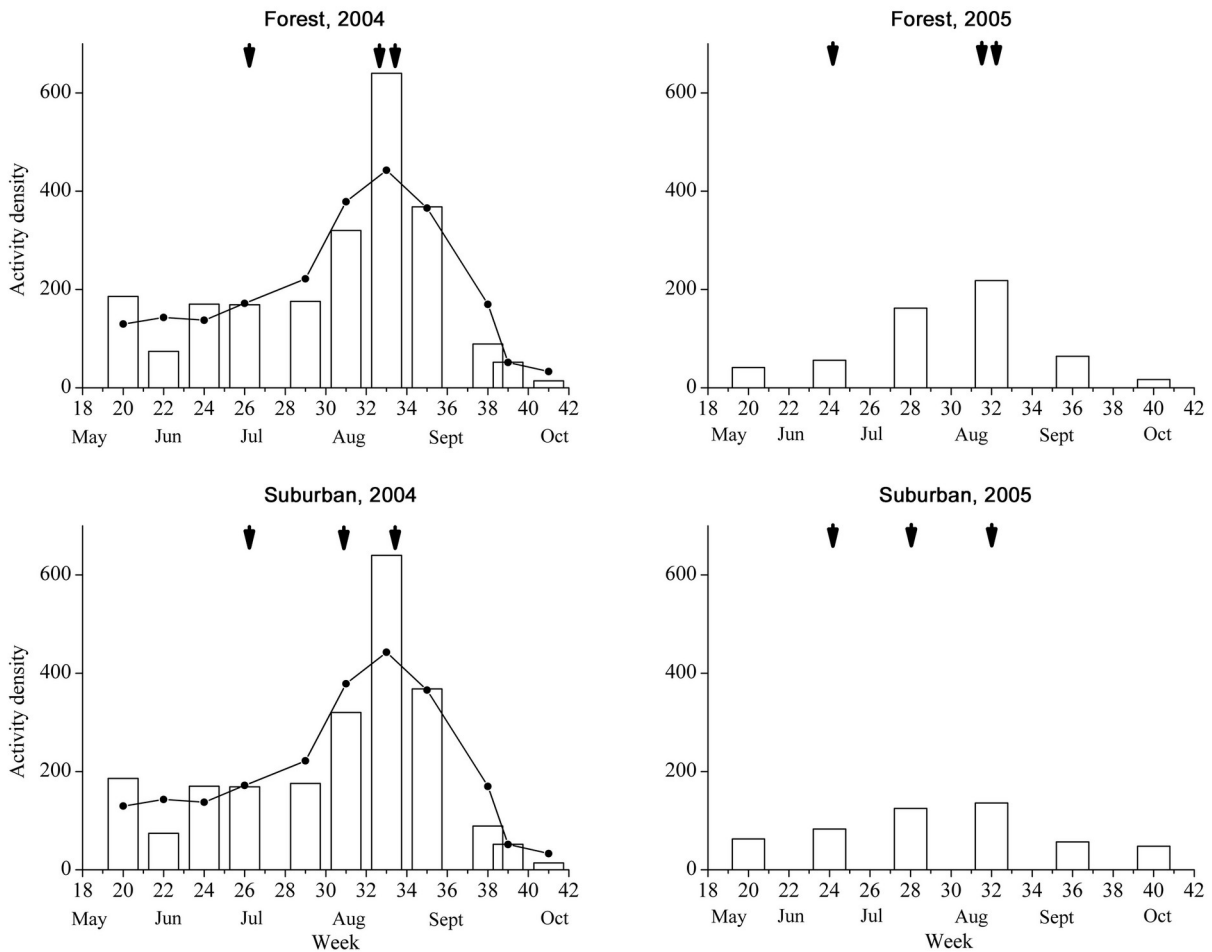
Abax ater

Figure 2.2.3. Seasonal dynamics of *Abax ater* at the three urbanisation stages (original forest, suburban, and urban forest remnants). Black arrows indicate the start, the peak and the end of the main activity periods, respectively. Bars indicate activity density (no. of individuals/trap \times fortnight) from start to end of sampling. Line on 2004 panels indicates running means of three weeks (and thus start on 2nd sampling occasion and ends earlier than sampling did). Running means were not calculated for 2005, due to the few sampling occasions.

Discussion

Based on their activity densities, all of the six studied forest species were able to maintain large and continuously surviving populations in urbanised (*C. nemoralis*, *P. melanarius*) or suburbanised (the remaining four species) habitats. This indicated that such habitat fragments could provide a way for species survival at the landscape level even under urbanised conditions, although it might depend on the dispersal ability of the species. Species with constant activity (*C. hortensis*, *C. coriaceus* and *A. ater*) had high activity in autumn, while species with flexible seasonality (*N. brevicollis*, *C. nemoralis*, and *P. melanarius*) had a bimodal activity pattern with high activity periods in both

spring and autumn. *A. ater* shows a similar high activity pattern in autumn in Paris, France (Vergnes et al. 2013). In the case of *N. brevicollis*, the forest patches in the urbanised habitat had higher activity densities; therefore, they can even serve as population sources, not sinks. This is an interesting phenomenon, because urbanised habitats are often considered sink habitats (e.g., Padilla & Rosewald 2015). Carabids in the northern temperate region are generally active during spring and late summer (Penney 1969, Thiele 1977). This is generally attributed to the food requirements of egg-laying females. Adult-overwintering species emerge in spring, and are soon in reproductive condition producing a spring activity peak. Many otherwise polyphagous species require protein at this life stage (Mayntz et al. 2005), and ground beetles get this from suitable prey, mostly invertebrates (Larochelle 1990). Invertebrate activity in spring is influenced mainly by temperature, which is more capricious in spring than in summer-autumn. Consequently, more between-site and between-year variation in the early seasonal activity period can be expected for such species than for those breeding late summer-early autumn. The late summer-early autumn peak is mostly caused by species overwintering as larvae, completing their development in spring, then emerge and reproduce. Several species reproduce more than once, creating two reproductive periods that sometimes become two “reproductive subpopulations” (Kádár et al. 2015). The same species can have different habitat preferences in different parts of their distribution range (Tyler 2008) and their activity patterns can also be different (Butterfield 1986, Matalin 2006) which makes studies of seasonal activity in different locations worthwhile. However, studies rarely go beyond registering the fact that there can be/are differences in seasonal dynamics (e.g., Matalin 2006). Seasonal dynamics are influenced by both inherent rhythms and random local events, like cold spells or rainy periods. Such “noise” has the potential to confound the underlying pattern, and the use of a standardised, quantitative method to describe seasonal activity followed here (Fazekas et al. 1997) allows to reduce the impact of local “noise” on the pattern, making between-site comparisons more feasible and interpretable. All species studied here showed clear differences in seasonality, sometimes also between the different studied habitats.

Two main groups could be distinguished. The first one consisted of the species with constant seasonality (*C. hortensis*, *C. coriaceus* and *A. ater*), in which the activity profiles among sites and years did not differ significantly. *C. hortensis* showed a consistent activity pattern with slight unimodality among the years and sites. This consistency was also documented by Jørum (1976a). The autumn activity did not decrease at the end of the trapping period, corresponding to Schjøtz-Christensen’s (1968) findings in Mols, in the Jutland Peninsula of Denmark. This species overwinters as larvae, and has low dispersal power, so its presence indicates suitable habitat conditions for individual development and the maintenance of a self-supporting population. *C.*

coriaceus showed consistent unimodal activity pattern like *C. hortensis*. Kålås (1985) found a unimodal activity pattern also in western Norway, but the activity peak occurred a month earlier. In Jutland, however, the same species had a bimodal activity pattern (Jørum 1976a) with a second activity peak in late September. In Hungary, the activity period of *C. coriaceus* preceded that of *C. hortensis* (Kádár et al. 2015). The unimodal activity pattern by *A. ater* was similar to that found in Jutland (Jørum 1976a).

The second group consisted of the species with flexible seasonality (*N. brevicollis*, *C. nemoralis* and *P. melanarius*), in which there were substantial differences among sites and years. *N. brevicollis* showed between-year constancy in the urban park, but not in the suburban and rural forest habitats. The bimodal activity curve of *N. brevicollis* was clearly observed at Sorø. The characteristic diapause in July and August corresponds to other findings in Denmark (Jørum 1976a, b) and Norway (Kålås 1985). It can be explained by the photoperiod-governed aestivation that characterises this species (Thiele 1969). In five of the six year-samples, the autumn activity density was higher than the spring one. The temporal changes in the activity density were fast, because the emergence of teneral adults leads to a rapid increase in the number of individuals (Penney 1969). These individuals might migrate to other habitats and could have caused the time lag in the increase of the number of individuals in the suburban area. The late activity peaks in the suburban and forest habitats indicated that these sites are less favourable for this species, and therefore these sites could be sink habitats. *C. nemoralis*, a spring breeder, showed bimodality with varying tendencies among sites. The peak activity periods were in June and October, which corresponds to the findings by Kålås (1985) in western Norway. A smaller bimodality seems to occur also in the Netherlands (Turin 2000), but in northern Scandinavia the species develops over two years (Lindroth 1985). It is likely that the size of the second peak depends on temperature: in warmer years, more newly emerged adults show surface activity. *P. melanarius* showed unimodal, or fused bimodal activity pattern with activity peak varying between July and August, corresponding to the findings in Jutland (Jørum 1976a). However, in Norway, the high activity period occurs a month earlier (Kålås 1985). The same species shows a biennial life-cycle in Hestehave at Kalø, Jutland (Jørum 1980), probably just coincidentally because of the extreme climatic conditions during the specific study period. Indeed, Matalin (2006) documented large variations in the life-cycle of *P. melanarius* probably driven by climatic differences. Females of this species can overwinter and reproduce again the following spring. Jørum (1980), for example, found 30% of old females have eggs relatively early in the season, which could cause the observed activity pattern in our study.

Considering all the six species investigated here, the overall activity density was highest in the rural forest and urban park in both years. In the suburban forests, a less consistent activity pattern was

found. High (early) spring activity occurred regularly in species in the urban park. In suburban forests, the pattern was less consistent: there was broad variation in the occurrence of spring and autumn activity periods. In the rural forest, autumn activity peaks were more frequent. There could be a simple cause, such as increased temperature in cities which makes urban forest fragments warmer than the continuous forests (Landsberg 1981).

2.3 Impacts of urbanisation on the developmental instability of ground beetle populations

Urban ecosystems have been formed after the “colonising” human populations profoundly transform the original habitats and remained under the consistent and pervasive anthropogenic influence (McIntyre et al. 2001). At the assemblage level, the effects of human activities on abundance, species richness and diversity are not always negative (Magura et al. 2010a, 2010b). Modified urban landscapes might have increased habitat diversity, resulting in higher species richness than in the less disturbed and more rural sites (Eversham et al. 1996, Elek & Lövei 2007). Habitat specialist species (i.e., forest specialists) are more affected by urbanisation than generalists, and decline in urban habitats (Elek & Lövei 2007, Magura et al. 2010a). However, the focus of these studies is at the supra-individual level with their inevitable time constraints: effects on populations and assemblages need one or more generations to unfold (Magura et al. 2008). However, organisms/individuals react to urbanisation-driven conditions in their habitats faster at lower organisational levels, including behavioural or physiological components. These parameters seem to be promising to detect less drastic effects than population extinction (Janin et al. 2011). Two potentially useful measures are the fluctuating asymmetry (Palmer & Strobeck 1986) and the physiological condition (Marshall et al. 1999) reflecting environmental stress throughout individual development (Parsons 1992) and which, in invertebrates, often spans several months, therefore it provides a quick snapshot about the environmental conditions.

2.3.1 No increase in fluctuating asymmetry in ground beetles as urbanisation progresses

Several morphological traits are symmetrical, and theoretically should display perfectly identical halves. Deviations from this ideal state lead to different types of asymmetry (Palmer & Strobeck 1986, 1992). One of these, the fluctuating asymmetry (FA) is a measure of the developmental stability of an organism and refers to random and subtle deviations from perfect bilateral symmetry (Palmer & Strobeck 1986, 1992). FA can increase when environmental stress disrupts developmental processes that normally promote symmetrical growth (Floate & Fox 2000). FA was suggested as a cost-effective indicator of environmental quality or stress (Valentine et al. 1973, Clarke & Ridsdill-Smith 1990, Clarke 1993, 1994). The applicability of FA to assess habitat quality has been widely discussed (Clarke 1995, Møller 1995, Leung & Forbes 1996, Møller & Thornhill 1997, Leung et al. 2000, Van Dongen & Lens 2000), but remains controversial. While a wide range of organisms and characters show increased FA due to exposure to a variety of environmental stressors (Hendrickx et al. 2003, Labrie et al. 2003, Weller & Ganzhorn 2004, Vilisics et al. 2005, Garnier et al. 2006, Henriquez et al. 2009), in some other cases, the approach seems an inappropriate indicator of environmental stress (Floate & Coghlin 2010).

To extend the methodological toolkit examining the effects of urbanisation, the usefulness of FA was tested for bilateral traits to signal habitat quality of/for ground beetles living in forested habitats in different urbanisation stages. First, we examined which of the commonly suggested morphological characters showed fluctuating (or true) asymmetry in ground beetles. Second, we examined the behaviour of these characters, and whether they showed consistency (*sensu* Soulé 1967) in their reaction to the different levels of disturbance. Furthermore, we tested whether females were more sensitive than males to changes in habitat quality (Bots et al. 2009). It is known that females need more resources than males for reproduction, because they have to successfully form and lay fertile eggs. Fitness in females is often size-related and profoundly influenced by conditions during larval development (McCabe & Partridge 1997). We hypothesised that females were more sensitive than males to changes in habitat quality, stress or disturbance during their larval development resulting in higher levels of FA. This hypothesis would predict a higher level of FA in females than males. Finally, we tested whether common ground beetle species showed a higher level of FA in more urbanised habitats than in the original, rural ones. This is a derivative of the *Habitat Disturbance Hypothesis* (Gray 1989), but the response parameter is different from Gray's, assuming that habitat quality is the highest in the forested area. With progressing urbanisation,

general conditions for forest-associated species deteriorate (Magura et al. 2010b). However, for some species, conditions may remain favourable, and they can have a lower level of FA in urbanised habitats as hypothesised by Weller & Ganzhorn (2004).

Methods

Measurement protocols

From the overall catch (10,314 individuals belonging to 43 species in 2004, and 4,961 individuals of 38 species in 2005, Elek & Lövei 2005, 2007), we selected species that *a*) were common in the forested area, and *b*) minimum 10 individuals were trapped in at least two of the three urbanisation stages during the first half of the season. Three carnivorous carabids fulfilled these criteria: *Carabus nemoralis* (Müller 1764), *Nebria brevicollis* (Fabricius 1792), and *Pterostichus melanarius* (Illiger, 1783). We selected beetle individuals randomly from the catch in April– June 2005: 137 individuals of *C. nemoralis* (56 males, 81 females), 152 individuals of *N. brevicollis* (21 males, 131 females), and 176 individuals of *P. melanarius* (100 males, 76 females). This sample size was adequate to test FA differences (Smith et al. 1982, Palmer 1994). The selected beetles were kept at -18°C in individual containers until the measurements were taken. The measurement of all morphological traits involved two independent mounting and photographing of the specimens (Palmer 1994). Before taking measurements, beetles were thawed, and individually put into a plastic Petri dish filled with small (diameter 0.08 mm) glass beads which allowed to arrange them into a standard, horizontal position using a plastic gauge. Beetles were placed under a stereomicroscope (Nikon SMZ 800, 10–63× magnification) mounted with a digital camera (Nikon Coolpix 4500); two photographs were taken using identical aperture and exposure, at maximum resolution (2272×1704 pixels, in JPEG format). These digital photos were used to measure (precision of 0.0001 mm) the studied morphological traits, with the assistance of the software ImageJ (Rasband 2003). We measured morphological characters used in earlier studies. These included eight metric and one meristic characters (Fig. 2.3.1.1): the length of the second (*antsegment2*) and third (*antsegment3*) segments of the left and right antennae (Labrie et al. 2003); the lengths of the left and right elytrae (*elytra*, Weller & Ganzhorn 2004); lengths of the first tarsi (*tarsus1*), the first (*tibia1*) and second tibiae (*tibia2*) on both sides (modified after Garnier et al. 2006); the distance between the end of the femur and the proximal (*proxi*) and distal (*distal*) spines on the two first femurs (adapted from Hendrickx et al. 2003) and the number of spines on the second tibia (*spine*, Labrie et al. 2003).

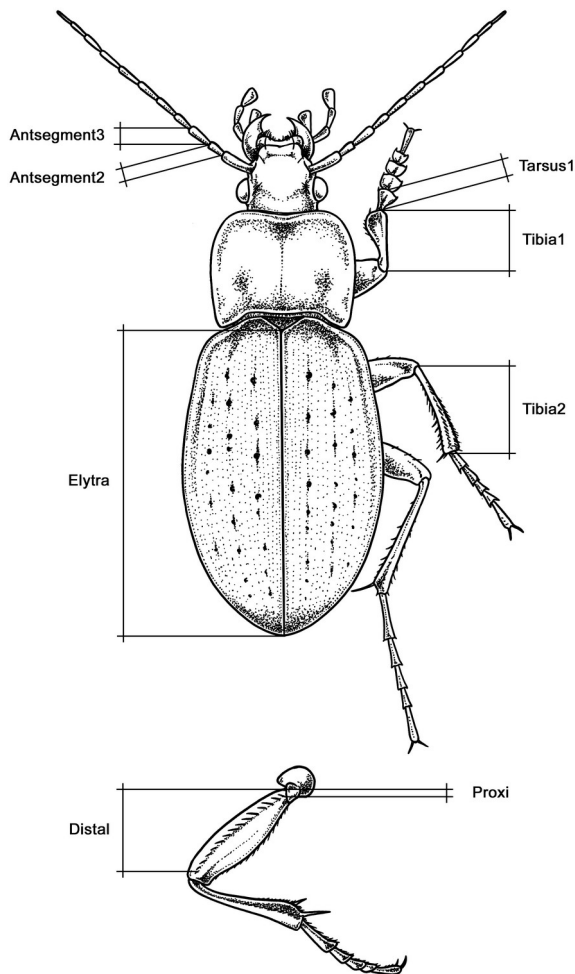


Figure 2.3.1.1 The measured morphological traits. Abbreviations: Antsegment2 & 3 – the length of the second, and third segments of the antennae respectively; Elytra – the length of the elytrae; Tarsus1 – the length of the first tarsi; Tibia1, & 2 – the length of the first and second tibiae respectively; Proxi, Distal – the distance between the end of the femur and the proximal and distal spines respectively on the first femur; Spine – the number of spines on the second tibia. Drawing credit: J. Ruzicková

Data analysis

The measured specimens were grouped according to urbanisation stage (rural, suburban, urban) and sex (female, male). The detection of outliers in the dataset was an important issue in the beginning of the analyses to control biases such as measurement error, directional asymmetry- or antisymmetry. Outliers were estimated by the Grubb and Dixon's test (corrected for small sample sizes) with the use of scatterplot for the average trait size. This protocol was applied for the raw data as well as for the estimated FA data. When consistency occurred in the two approaches, the data of that individual (a total of eight *C. nemoralis*, five *N. brevicollis* and four *P. melanarius*) were removed from the dataset. In order to exclude the developmental noise based on genomic stress, we tested if any of the traits showed directional asymmetry or antisymmetry. Directional asymmetry

(when bilateral variance is statistically significant among the sides, but the direction of the difference is consistent, i.e., the left side is consistently larger than the right one) was tested by factorial ANOVA for the overall samples and nested ANOVA (sides within individuals) for individuals as samples and for the estimation of skewness. Antisymmetry, when bilateral variance is statistically significant among the sides, but this variation is larger between the sides than between individuals (i.e., platykurtosis) was tested by calculating kurtosis. The true asymmetry (free from any developmental and statistical biases) of a morphological trait was confirmed by the Shapiro test for normality. An estimate of measurement error (ME) is essential for FA analyses (Palmer 1994). Measurements of each trait were compared using a two-way analysis of variance (ANOVA) with sides (right versus left) and individuals as factors. These tests measured whether non-directional asymmetry (i.e., FA, antisymmetry) could be distinguished from ME (Palmer 1994). If heterogeneity occurs in ME, it should be partitioned out in order to properly estimate the degree of FA (Palmer 1994).

The size dependence of FA within samples was tested by linear regression of the absolute difference of Right vs. Left ($|R - L|$) values against the elytra length as an independent measure of body size. The size-corrected and unsigned FA index was calculated as $FA = |R - L| / \text{mean} [(R + L)/2]$ (Vilisics et al. 2005 after Palmer 1994), where the unsigned difference is divided by the sample mean of the average trait size, where the sample referred to the combination of urbanisation stages and sexes. General linear mixed-effect models (LMM) were used to study the relationship between the response variables (FA) and the potential explanatory variables: the urbanisation stages and sex, as well as their interactions (Bolker et al. 2009). A nested random effect was added to account for the variance structure among the replicates (measurements 1 and 2) and individuals, to control the heteroscedasticity (Appendix of Elek et al. 2014) by measurement error: the individuals were nested in the replications. The differences among the categories of the tested factors were evaluated by multiple comparisons (with Tukey computed contrast matrices for several multiple comparisons procedures) after a single argument ANOVA for the tested model. For the meristic trait, G-test (log-likelihood ratio test) was used with Williams' correction to calculate the differences in the number of spines (i.e., frequencies) between the right and left side of the second tibia, using the R-scripts by Hurd (2010). When more than two morphological traits showed real asymmetry, a test of consistency in FA values was performed using the Kendall concordance analysis with a Bonferroni correction (Légendre 2005, Palmer 1994). Model parameters were estimated by using *nlme* (Pinheiro et al. 2012). Graphs were created using the *gplots* package (Warnes 2012) in R 2.15.2 (R Core Team 2020).

Results

Usefulness of morphological traits for asymmetry studies

Seven of the examined characters showed real FA in at least one of the selected carabid species (Table 2.3.1.1), but none of them was universally suitable. *Antsegment2* and *antsegment3* showed directional asymmetry in one and three species respectively; *elytra*, *proxi*, *distal*, *tarsus1* showed antisymmetry in two species, while *tibia1* for one species (Table 2.3.1.1). The *tibia2* showed antisymmetry and direction asymmetry for one species each. The character *spine* did not show any variation, and was unsuitable as a potential FA character.

Table 2.3.1.1 Performance of nine morphological characters as potential measures of fluctuating asymmetry in the selected species of carabids collected in pitfall traps at Sorø, Denmark, during spring 2005.

Morphological trait	Type of asymmetry		
	<i>Carabus nemoralis</i>	<i>Nebria brevicollis</i>	<i>Pterostichus melanarius</i>
<i>antsegment2</i>	fluctuating	directional (R<L)	fluctuating
<i>antsegment3</i>	directional (R<L)	directional (R<L)	directional (R<L)
<i>elytra</i>	antisymmetry	fluctuating	antisymmetry
<i>proxi</i>	fluctuating	antisymmetry	antisymmetry
<i>distal</i>	fluctuating	antisymmetry	antisymmetry
<i>tarsus1</i>	antisymmetry	antisymmetry	fluctuating
<i>tibia1</i>	fluctuating	fluctuating	antisymmetry
<i>tibia2</i>	fluctuating	antisymmetry	directional (R<L)
<i>spine</i>	no variation	no variation	no variation

Consistency of the asymmetry profiles within species

The analysis of concordance for *C. nemoralis* showed that there was no relationship among the traits showing real asymmetry ($W = 0.15$, $p = 0.63$). The test of the contribution of the traits to the overall concordance (Table 2.3.1.2) revealed that the asymmetries of the studied morphological traits were independent of each other.

Assessment of fluctuating asymmetry among different species, urbanisation stages and sexes

Asymmetry for proximal distance of spines on the femur in *C. nemoralis* was significantly influenced by the interaction of the urbanisation stage and sex (Table 2.3.1.3). The degree of the asymmetry for forest females was lower than for females in the urban park ($T_{169} = 2.269$, $p = 0.024$, Fig. 2.3.1.2). The asymmetry of the second tibia length was different by urbanisation stage only

(Table 2.3.1.3), and was higher in the rural forest than in the urban park ($T_{169} = -1.67$, $p = 0.096$, Fig. 2.3.1.2).

Table 2.3.1.2. Summary table of concordance analysis for *Carabus nemoralis*. The result of the global analysis is given for traits, the posterior test of the contribution of individual judges (morphological traits) to the overall concordance. Legend: W – Kendall's coefficient of concordance; p – permutational probabilities, uncorrected; cor.-p. – permutational probabilities corrected, calculated only if there are more than one group.

Morphological trait	Concordance/congruity
<i>antsegment2</i>	$W=0.16/ p=0.54/ \text{cor.-p.}=1$
<i>antsegment3</i>	no true asymmetry detected
<i>elytra</i>	no true asymmetry detected
<i>proxi</i>	0.12/0.85/1
<i>distal</i>	0.17/0.44/1
<i>tarsus1</i>	no true asymmetry detected
<i>tibia1</i>	0.13/0.86/1
<i>tibia2</i>	0.16/0.53/1

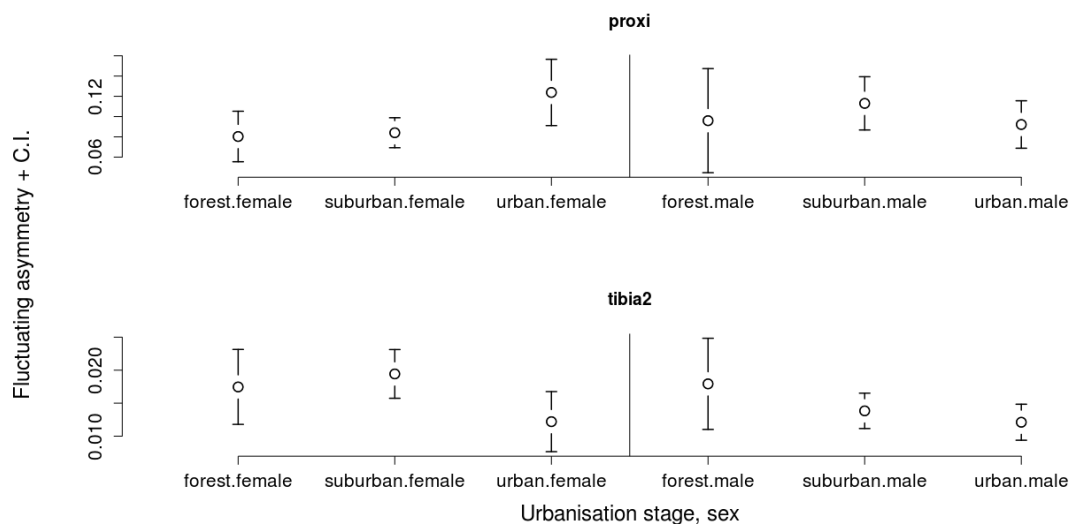


Figure 2.3.1.2 Distribution of asymmetry index for *proxi* and the *tibia2* in male and female *Carabus nemoralis* in the studied urbanisation stages. Data are means; vertical lines indicate $\pm 95\%$ confidence intervals.

In the case of *N. brevicollis*, the asymmetry of the first tibia was higher ($T_{277} = 8.70$, $p = 0.000$) in females than males. Females in suburbanforest and urban park had higher asymmetry ($T_{277} = -2.30$, $p = 0.02$; $T_{277} = -2.56$, $p = 0.01$ respectively) than males, while the (rural) forest males were unaffected (i.e., confidence interval included zero, Fig. 2.3.1.3). The interaction between sex and urbanisation stage was also significant (Table 2.3.1.3).

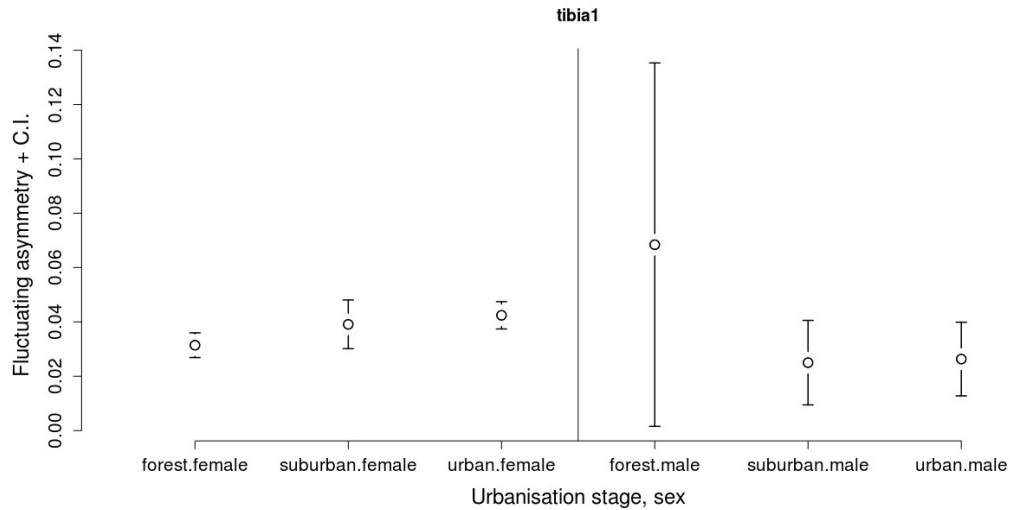


Figure 2.3.1.3 Distribution of asymmetry index for the tibia1 in male and female *Nebria brevicollis* in the studied urbanisation stages. Data are means; vertical lines indicate \pm 95% confidence intervals.

For *P. melanarius*, the asymmetry for first tarsus length was significantly influenced by the urbanisation stage; the interaction of urbanisation stage and sex was marginally significant (Table 2.3.1.3). The FA value for males was higher in the suburban forest ($T_{245} = 2.081$, $p = 0.038$) than either in the rural ones or urban park (Fig. 2.3.1.4).

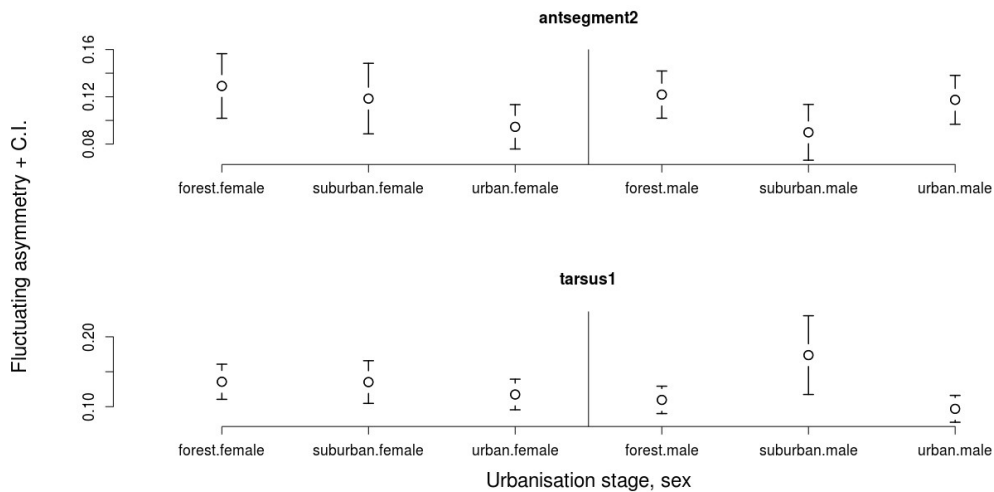


Figure 2.3.1.4 Distribution of asymmetry index for antsegment2 and tarsus1 in male and female *Pterostichus melanarius* in the studied urbanisation stages. Data are means; vertical lines indicate \pm 95% confidence intervals.

Table 2.3.1.3. Major results of linear mixed-effect models relating urbanisation stages and sexes to fluctuating asymmetry in ground beetles collected in pitfall traps at Sorø, Denmark, spring 2005. Significant values are in bold. Complete table available in Elek et al. (2014).

Morphological trait/species	<i>df.</i>	<i>F</i>	<i>p</i>
<i>Carabus nemoralis</i>			
proxi			
<i>intercept</i>	1, 169	369.468	< 0.0001
<i>Site</i>	2, 169	1.133	0.324
<i>Sex</i>	1, 169	0.454	0.501
<i>Site:Sex</i>	2, 169	3.449	0.034
<i>sd (random effects residuals)</i>			0.08
tibia2			
<i>intercept</i>	1, 169	352.753	< 0.0001
<i>Site</i>	2, 169	4.011	0.019
<i>Sex</i>	1, 169	2.673	0.103
<i>Site:Sex</i>	2, 169	1.396	0.25
<i>sd (random effect residuals)</i>			0.013
<i>Nebria brevicollis</i>			
tibia1			
<i>Intercept</i>	1, 187	285.639	<0.0001
<i>Site</i>	2, 187	2.292	0.102
<i>Sex</i>	1, 187	4.296	0.039
<i>Site:Sex</i>	2, 187	3.334	0.037
<i>sd (random effect residuals)</i>			0.027
<i>Pterostichus melanarius</i>			
tarsus1			
<i>Intercept</i>	1, 245	489.739	<0.0001
<i>Site</i>	2, 245	4.578	0.011
<i>Sex</i>	1, 245	1.887	0.17
<i>Site:Sex</i>	2, 245	2.419	0.091
<i>sd (random effect residuals)</i>			0.09

Discussion

Usefulness of morphological traits for FA studies

Most of the published FA studies (Hendrickx et al. 2003, Labrie et al. 2003, Garnier et al. 2006, Henríquez et al. 2009) were performed on a single species, using one or several closely related traits. The relationship between the selected traits was not always analysed. In this study, seven out of nine morphological traits showed true asymmetry in one or more of the common carabid species. The character *tibia2* showed directional and antisymmetry in one species each, similar to another European ground beetle, *Carabus soleri* (Garnier et al. 2006). This suggests that this type of asymmetry may have a genetic background. Two morphological traits (*antsegment2*, *tibia1*) that showed real asymmetry in two studied species could be useful in further FA studies.

Sex-specific differences in fluctuating asymmetry

Fitness of females is often size-related and profoundly influenced by conditions during larval development (McCabe & Partridge 1997). Most of the published studies on FA (Hendrickx et al. 2003, Labrie et al. 2003, Weller & Ganzhorn 2004, Garnier et al. 2006) did not consider sex as a factor in their analysis. Only Vilisics et al. (2005) and Henríquez et al. (2009) included this variable, but they found no effects on isopods and carabids, respectively. In our study, *C. nemoralis* and *N. brevicollis* females were more asymmetric than males, indicating that females might indeed be more sensitive to disturbance than males.

Fluctuating asymmetry and urbanisation

Higher developmental instability in more urbanised habitats was reported from Northern Germany (Weller & Ganzhorn 2004) and this can be considered to support for the *Habitat Disturbance Hypothesis* (Gray 1989). Although FA in the length of the *tibia2* in *C. nemoralis* showed differences among the studied urbanisation stages, this asymmetry was higher in the forest than in the other urbanisation stages, while *tarsus1* showed lower FA values in the urban stage than elsewhere for *P. melanarius*. Finding similar inconsistencies, Weller & Ganzhorn (2004) speculated that habitat size and the degree of isolation could play a role in this phenomenon. Weller and Ganzhorn (2004) also suggested that the species occurring at all studied sites are more "robust" and are less affected by

urbanisation-related stress than species which do not occur at all studied sites. If this suggestion is correct, the less common species, in general, should show a higher degree of FA than the common ones, which remains to be tested. We did not find unequivocal support for the hypothesis that as urbanization progresses, the conditions create higher levels of FA in ground beetles present in more than one urbanization stage. This makes it difficult to suggest that measuring FA is useful to indicate environmental disturbance in ground beetles. Females showed a higher level of FA than males, which underline the separation of sexes in further studies. The theoretical advantages of using within-individual characters as markers of habitat quality are still upheld, but the question of whether measuring FA in carabids is useful in this context remains open.

2.3.2 Sex-specific interaction of body condition and asymmetry in carabids in distinct urbanisation stages

At the individual level, changes in body condition could also be used to characterise habitat quality. This could even be a more flexible signal as condition indices provide a snapshot about the physiological state of an individual and could indicate recent foraging success (Marshall et al. 1999, Ball et al. 2015) that is affected by changes in resource availability or environmental stress. Using materials collected in the Danglobe Project (Elek & Lövei 2005) in 2005, we tested whether such changes were reflected in body conditions of ground beetles' individuals. It is assumed that as urbanisation progresses, environmental conditions of ground beetles would gradually deteriorate, and this would be reflected in decreasing body conditions. We hypothesized a sex-specific reaction to the same factors, assuming that females would be more sensitive than males, due to their higher energy needs related to reproduction. Thus they are about to maximize their energy reservoirs by building fat bodies. Therefore, we expected that the females have better conditions than males, though both of them would respond negatively to urbanisation (i.e., show lower conditions in more urbanised habitats than in the forest). Furthermore, the level of fluctuating asymmetry influences on body condition was examined in a sex-specific way, suggesting that the condition will decrease as urbanisation progresses and this relationship is stronger for females than males.

Methods

Data collection and measurements

For evaluation, we selected individual beetles *ad hoc* from the catch in April–June, 2005 using the material collected in the Danglobe Project. The sample included 136 (out of the 155 three-month total) individuals of *C. nemoralis* (59 males, 77 females); 152 (out of the 400) individuals of *N. brevicollis* (14 males, 138 females) and 176 (out of the 356) individuals of *P. melanarius* (98 males, 78 females). Measurements and morphological traits used were estimated as written in the Chapter 2.3.1.

Data analysis

To characterise physiological condition of the individuals, we used the residual index (Gould 1975), where the body mass is regressed on body size, and the residuals provide an estimate of condition (e.g., Jakob et al. 1996). For this index, the elytra length was used as a proxy for body size (Lagisz 2008, Knapp & Knappová 2013). The length of the right elytra was measured with a precision 0.001 mm. The body mass was measured using an electronic balance, to a precision of 0.1 mg. Two independent measurements were taken for every trait. Data on traits showing real fluctuating asymmetry (FA, Palmer 1994) were considered for testing the condition-asymmetry relationship based on a previous study (Elek et al. 2014). We calculated a size corrected and unsigned FA index, where the unsigned difference was divided by the sample mean of the average trait size (Palmer 1994). We calculated a linear regression of the body mass on body size, separately for each species and sex. The residual values from the model output were compared by general linear models among the sites and sexes.

We tested differences in condition (residual index values as a response variable) by a general linear model (GLM) with the habitats and sexes as fixed factors and Gaussian error structure. The differences among the levels of the tested factors (habitat type and sex) were evaluated by multiple comparisons with Tukey contrasts for multiple comparisons of means. The condition index on FA values was tested using local polynomial regression models (LOESS) per habitat types and sexes for the species where the models showed significant effects (Cleveland et al. 1992). The LOESS fits a regression surface to data through multivariate smoothing. The dependent variable is smoothed as the function of the independent variable(s) similarly to the moving average was computed in the time series analysis. The fundamental form is $y_i = g(x_i) + \varepsilon_i$, where the “y” is the dependent, the “x” is the independent variable, ε_i is the error term and the “g” is the smoothing function of the independent variables. With local fitting a wider class of smoothing functions can be estimated than we can expect from any specific parametric class of functions (Cleveland & Devlin 1988). The analyses were carried out in R 2.11.1 (R Core Team 2020) using the packages *multcomp* (Hothron et al. 2008), *lattice* (Deepayan 2008) and *agricolae* (Mendiburu 2010).

Results

Condition index in relation to urbanisation stage

Body conditions of the three species reacted differently to urbanisation. *C. nemoralis* had the best condition in the urban park, demonstrating a significantly higher index here than in either of the other two habitats (Fig. 2.3.2.1, Table 2.3.2.1). *N. brevicollis* also had the highest index in the urban park, somewhat (but not significantly) lower in the rural forest and significantly lower in the suburban forests (Fig. 2.3.2.1, Table 2.3.2.1). *P. melanarius* showed better condition in the suburban forests than in either the urban park or rural forest habitats; forest beetles were also in better condition than in urban ones (Fig. 2.3.2.1, Table 2.3.2.1).

Table 2.3.2.1. Comparison of the physiological condition (characterised by the residual index) of three common ground beetle species by site or sex. Numbers are means \pm s.d. The number of individuals measured are in parentheses. Significance symbols: ***-0.000, **-0.001, *-0.01, ' - 0.1

Species	Condition index			Comparison
	Forest	Suburban	Urban	
<i>Carabus nemoralis</i>	-6.93 \pm 89.34 (30)	-13.52 \pm 90.48 (64)	25.55 \pm 91.6 (42)	U>S*; U>F'
<i>Nebria brevicollis</i>	-0.53 \pm 10.22 (38)	-6.56 \pm 14.73 (29)	2.48 \pm 14.1 (85)	U>S**
<i>Pterostichus melanarius</i>	2.27 \pm 21.6 (77)	20.68 \pm 31.16 (27)	-10.19 \pm 23.8 (72)	S>F**, F>U**, S>U***
		Female	Male	
<i>Carabus nemoralis</i>		23.41 \pm 102.22 (77)	-30.55 \pm 64.4 (59)	F>M***
<i>Nebria brevicollis</i>		1.19 \pm 13.63 (138)	-11.78 \pm 7.3 (14)	F>M***
<i>Pterostichus melanarius</i>		4.28 \pm 30.65 (78)	-3.41 \pm 21.6 (98)	n.s.

Condition index in females vs. males

Females of *C. nemoralis* and *N. brevicollis* showed significantly better condition than males did (Fig. 2.3.2.1, Table 2.3.2.1). Urban females of *C. nemoralis* were in better condition than males. In the case of *N. brevicollis*, both urban and forest females were in better condition than males from the corresponding sites, but the overall difference, while in the same direction, was not significant (Fig. 2.3.2.1, Table 2.3.2.1).

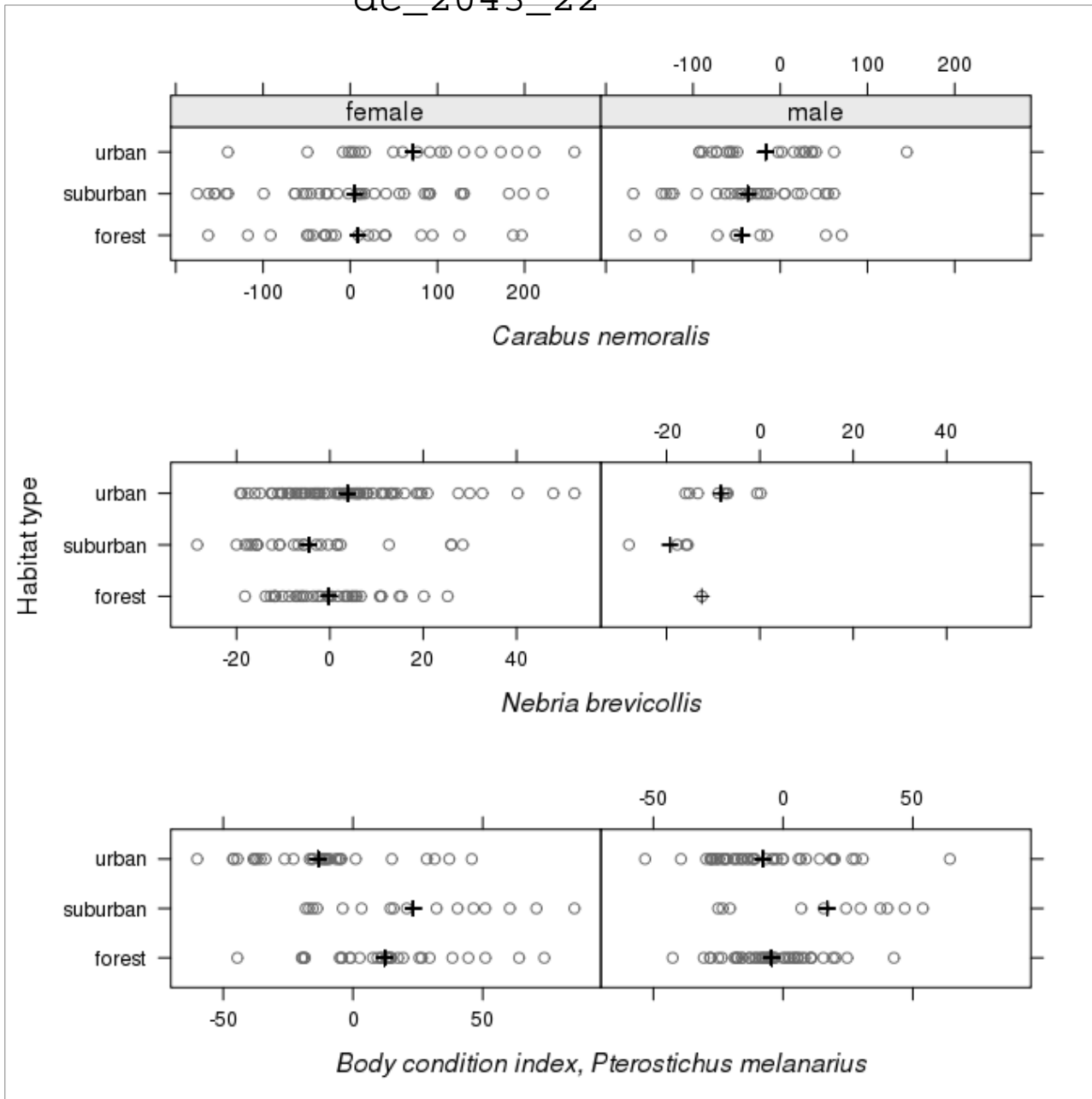


Figure 2.3.2.1 Distribution of condition indices in males and females of three carabid species along the urbanisation gradient. The crosses denote the arithmetic mean of the condition index.

Interaction between fluctuating asymmetry and condition

There was generally a negative relationship between the FA values and the condition index. In *C. nemoralis*, the slope of the relationship was steeper in the more urbanised habitats (suburban forest fragments and urban park) than in the rural forest (Fig. 2.3.2.2). Both sexes showed a similar negative relationship (Fig. 2.3.2.2). In *N. brevicollis*, the slope was less steep in the rural forest than the other two habitats (Fig. 2.3.2.3). Females with higher FA had worse body condition than males in both suburban forests and urban park (Fig. 2.3.2.3). No consistent pattern was found between FA and condition for *P. melanarius* for either habitat types or sex.

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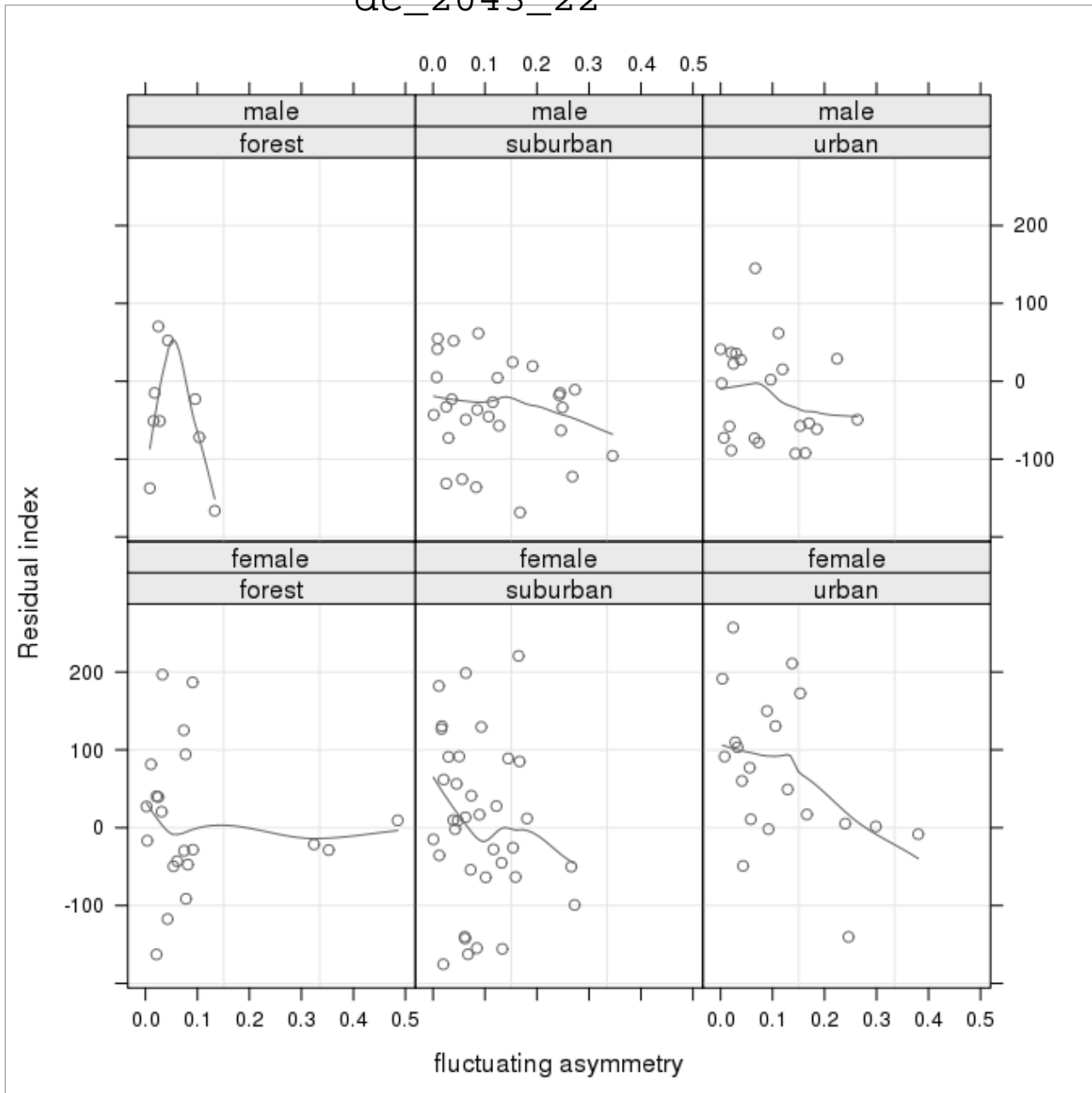


Figure 2.3.2.2 The relationship between fluctuating asymmetry and body condition of *C. nemoralis* along the urbanisation gradient and between males and females. The line is the locally weighted regression between the two variables ($\lambda = 1$, $\alpha = 0.9$)

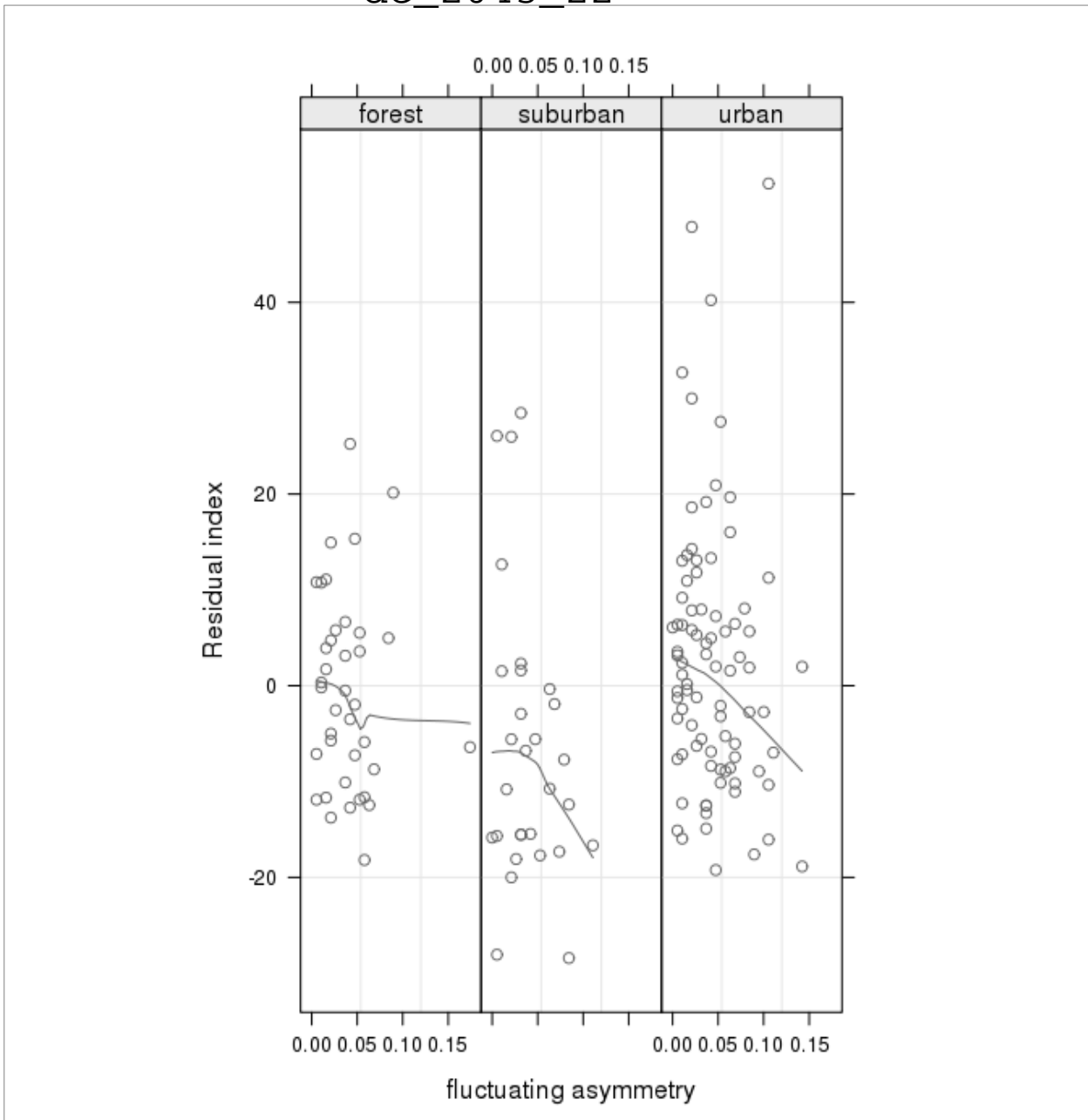


Figure 2.3.2.3 The relationship between the fluctuating asymmetry values and body condition of *N. brevicollis* along the urbanisation gradient. The line is the locally weighted regression between the two variables ($\lambda = 1$, $\alpha = 0.9$)

Discussion

The body condition of the individuals would be better in the less urbanised habitats (i.e., rural forest) than in forest fragments in urbanised areas. However, the pattern revealed contradicted this: individuals of two common species, *C. nemoralis* and *N. brevicollis* showed better body conditions in the urban park than in the other habitats. The third one, the generalist predator *P. melanarius* did not show the best condition in the rural forest either. While there are organisms where body condition is inferior in fragmented habitats, like treecreepers in Finnish forests (Suorsa et al. 2004), or salamanders in California (Karraker et al. 2006), this is not universal. Wintering wood mice (*Apodemus sylvaticus* L. 1758) in Spain did not have worse body condition in forest fragments vs. continuous forest (Diaz et al. 1999), and several small mammal species in the Atlantic forests of Brazil have even better body condition in fragmented than non-fragmented habitat (Puttker et al. 2008). Also, landscape management in Sweden did not influence body conditions of wolf spiders as expected: the large, homogeneous fields were more favourable than organically managed, small fields (Öberg 2009). Therefore, the effect seems to be context- and species-dependent. We found that the body condition of females in *C. nemoralis* and *N. brevicollis* was higher than that of males. This pattern was similar to those found for fluctuating asymmetry in females vs. males of *C. nemoralis* and *P. melanarius* (Elek et al. 2014): females had lower levels of fluctuating asymmetry than males. Females usually need more resources than males for reproduction, because they have to successfully form and lay fertile eggs (e.g., Uetz et al. 2002), and it is plausible to assume that inferior-quality females do not survive to reproduce (*sensu lato* Hendrickx et al. 2003). Similarly, the high level of true asymmetry can be deleterious for individuals and can also influence the larval-to-adult survival (Lens et al. 2002). Consequently, the surviving population could contain the individuals who survived these stress factors and are a robust subset of the original population, whose asymmetry is now relatively unaffected by the current stressors (Floate & Fox 2000, Floate & Coghlin 2010). The wide scatter of condition in individuals with a low degree of FA could reflect the variable nutritional conditions experienced. However, the generally low condition of individuals with high FA could indicate the lower quality of these habitats. This negative relationship was steeper in more urbanised habitats. This indicated that habitat quality was indeed lower in more urbanised habitats, and consequently, individuals with higher FA were able to cope less well than higher quality (less asymmetric) ones. We found a clear, consistent trend in our data, unlike Hendrickx et al. (2003).

2.4 Conclusions

The most important achievements of the documented work on urbanisation can be assumed as:

- 1) There are two major groups of carabids which are exposed to significant changes at the community level by urbanisation: the number of forest species and their relative frequency significantly increased from the urban park to the rural forest habitats. Also, the number of open-habitat species was significantly higher in the urban park than in the suburban and rural forests. In addition, the smaller species were more abundant in urban remnants of the original forest. The larger, less mobile species were more abundant in the rural forest area. A possible cause of this, was the impact of the surrounding habitat matrix: the presence of extensive open habitats in the urban area. The matrix species had an impact on species richness patterns in forest fragments. Other impacts of masking habitat fragmentation and disturbance effects include microclimatic changes at edges, short-term crowding effects, and time lags.
- 2) Considering all the six studied species' seasonal activities, the overall activity density was the highest in the rural forest and urban park. High (early) spring activity occurred regularly in species in the urban park. In suburban forests, the pattern was less consistent: there was broad variation in the occurrence of spring and autumn activity periods. In the rural forest, autumn activity peaks were more frequent. This may have a simple cause, like increased temperature in cities, which made forest fragments in the urban park warmer than the continuous forests resulting increased activity regime for urban-dwelling carabids (e.g., Elek et al. 2017a, Lövei et al. 2018).
- 3) We did not find unequivocal support for the hypothesis that as urbanization progresses, the conditions create higher levels of FA in ground beetles present in more than one urbanization stage. This made it difficult to suggest that measuring FA was useful to indicate environmental disturbance in ground beetles. Females showed a higher level of FA than males, which warranted the separation of sexes in further studies of this type. Although the conceptual advantage of within-individual characters as markers of habitat quality have already confirmed, the usefulness of measuring FA for ground beetles is still under debate.
- 4) The results revealed that physiological condition could be a useful estimator of environmental conditions in urbanisation studies; and that the applied residual index for condition seemed an appropriate analytical tool. However, the inconsistency of the species' responses indicated possible confounding effects (i.e., larval development, seasonal differences in sex ratio and condition). The applied loess regression model to relate condition and FA revealed that the fragmentation of forest patches during urbanisation could indeed create less favourable conditions for ground beetles. Therefore we suggest using these estimators in combination (e.g., Elek et al. 2017b).

3. Context-specific responses of ground beetles to different forestry treatments

European forests are under pressure caused by the substantial anthropogenic modification, only 4% can be considered as undisturbed, where the natural processes and structural elements are dominant (European Commission 2021). Windthrows, forest fires as rare and coarse-scale disturbances and the spontaneous gap dynamics as a good example for frequent fine-scale disturbances may support the structural diversity of these forests either at the stand- or at the landscape level (Bengtsson et al. 2000). The majority of the European forests managed by rotation forestry systems characterised by even aged stand with low species richness, structural homogeneity and the lack of tree-related microhabitats such as large dead logs or veteran trees. The pervasive disturbance caused by rotation forest management had a remarkable negative effects on biodiversity and this process have enhanced by the progressive technical development in forestry (Bengtsson et al. 2000, Vanbergen et al. 2005, Hermy & Verheyen 2007). Although the negative effect of forestry on forest biota is well known, these managed forests may preserve high biodiversity including thousands of forest specialist species, large carnivores and special habitat types (European Commission 2021). Although there are many case studies concerning the specific effects of various forest management treatments, there are only few initiatives in the temperate zone (Knapp et al. 2014) that compare experimentally the effects of the treatments of multiple forestry systems on biodiversity (Paillet et al. 2010). Most evidence points to the variability of responses within and across taxa (Irwin et al. 2014, Sabatini et al. 2016), suggesting that organism groups strongly related to specific microhabitats or structural conditions are influenced negatively by forest management (Wolters et al. 2006, Paillet et al. 2010). The major motivation here is to explore the effects of different forestry practices on the assemblages of carabids and on their selected species populations. I presumed that the carabids of those treatments where the canopy does not changed substantially resemble more to the carabid assemblages of the original forests based on their species composition and diversity. In addition, there is a debate whether the suggested indicators are suitable for the use in close-to-nature forestry and also describe the most suitable indicators (either species or other taxonomic surrogates) for various forestry treatments.

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

The response of ground beetles was assessed to site conditions modified by silvicultural practices to compare the effect of different forest management approaches on biodiversity. Within the framework of biodiversity and conservation studies in managed forests, species composition, richness, alpha diversity indices and abundance are the simplest measures for biodiversity based on the species taxonomic identity of the individuals (Magura 2017). Previous studies revealed that species composition have changed the most, while changes in species richness and abundance among forestry treatment were equivocal mostly connected to the annual variation (Heikkala et al. 2016, Koivula et al. 2019, Yamanaka et al. 2021). Any changes in the taxon-based measures for ground beetle assemblages will reflect carabids' functional role in the forests due to the fact that their functional traits are highly connected with their taxonomic identity (Magura 2017, Magura & Lövei 2019). Schirmel et al. (2012) revealed that functional traits may contribute to trait-based environmental filtering in forming species communities with the premise of exploring the resources utilization, dispersal or reproduction. Although functional traits analysis can indirectly estimate the ecosystem functions, their use is more suitable for species' population level (Murray et al. 2017). In theory, functional diversity metrics can assure for exploring the effects of disturbance on community-level processes and changes in ecosystem function (Botta-Dukát 2018). With standardized methods for functional diversity, previous investigations (Schirmel et al. 2012, Murray et al. 2017, Nolte et al. 2017) have recently assessed the functional diversity responses to disturbance in various forested habitats and taxonomic groups. These studies revealed that the functional diversity of an assemblage represents a direct link between the environment and emergent ecosystem functions and can be taxon-dependent. Furthermore, Murray et al. (2017) also added that functional diversity cannot be assumed to have positive covariance with species richness due to functional redundancy where multiple species perform similar roles in an ecosystem. However, the proper use of functional trait and diversity measures on the impact of forest management types still needs to be clarified (Spake et al. 2016, Nolte et al. 2017). In a forest ecological experiment that follows randomized complete block design, the medium-term (up to four years after the implementation) effects of four forestry treatments were investigated in relation to rotation (Matthews 1991) and continuous cover forestry systems (Pommerening & Murphy 2004) on ground beetles. The major aims were to (i) explore how the taxon-based descriptors of carabid assemblages (composition, species richness, diversity and abundance) vs.

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

Methods

Study area

The study area is located in the Pilis Mountains (N 47° 40' and E 18° 54'), in the northern part of Hungary (Fig. 3.1.1a). The hills are at the elevation of 370–470 m a.s.l., with an annual precipitation of 600–650 mm and a mean annual temperature of 9.0–9.5 °C (Dövényi 2010). The bedrock of the area is limestone and red sandstone with loess deposits, forming a luvisol type soil. The investigated 40-ha-sized stand was an even-aged mature (80 years old) oak-hornbeam forest (Natura 2000 code: 91G0). The stand has been managed by shelterwood silvicultural system (Matthews 1991), where the height of the upper canopy layer at 21 m was dominated by sessile oak (*Quercus petraea* (Matt.) Liebl., height 21 m, diameter at breast height 28 cm) and a secondary canopy at 11 m contained mainly hornbeam (*Carpinus betulus* L.). Subordinate/Admixing tree species included turkey oak (*Quercus cerris* L.), beech (*Fagus sylvatica* L.), wild cherry (*Prunus avium* L.) and manna ash (*Fraxinus ornus* L.). The shrub layer was scarce; and ground cover was 30%, with *Carex pilosa* Scop. and *Melica unflora* L. as dominant herb species.

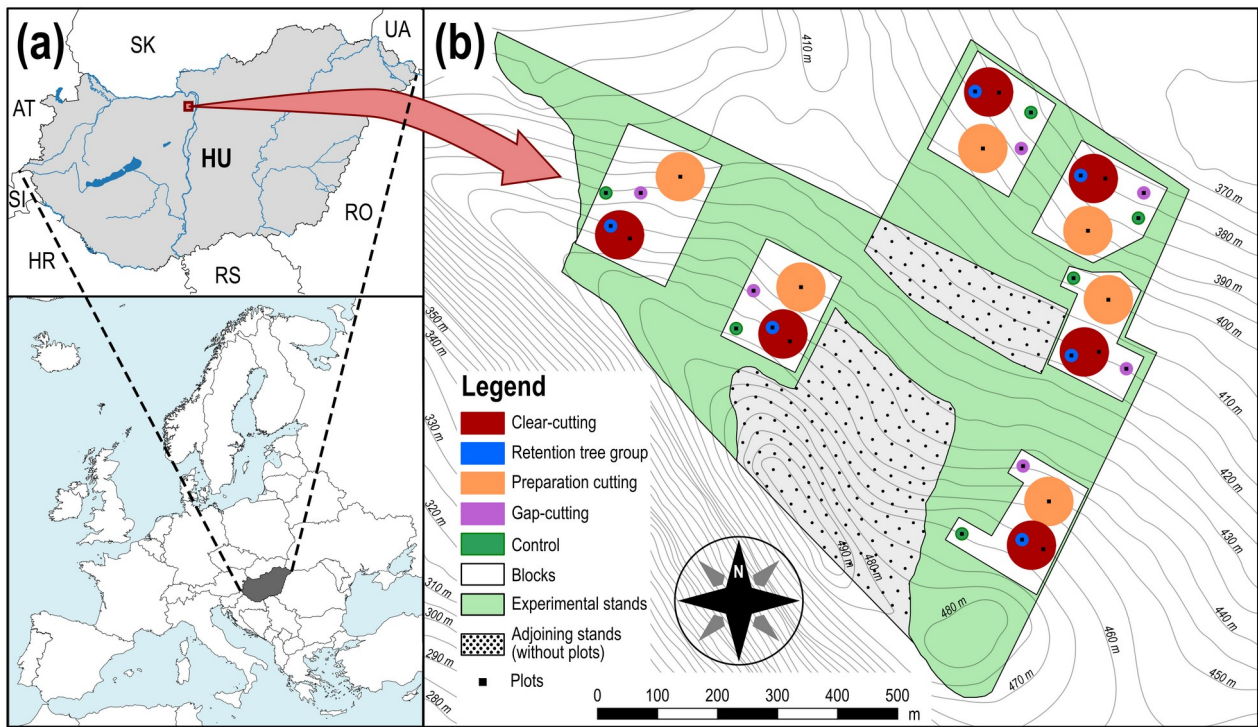


Figure 3.1.1 Map of the study area in the Pilis Mountains, Hungary and the design of the Pilis Forestry Systems Experiment.

Experimental design

Our study was the part of the long-term Pilis Forestry System Experiment (<https://piliskiserlet.ecolres.hu/en/node/1>) where four forestry treatments including their control (C) were established in 2014 with six-replicate blocks to explore the major effect of various treatments on forest organisms, such as plants, enchytraeids worms, spiders and ground beetles (Elek et al. 2018). We established five forestry treatments using a complete block design with six blocks as replicates (Fig. 3.1.1b): 1. Control (C): mature, closed-canopy stand without any treatment; 2. Clear-cutting (CC): all trees were cut and removed from a circular area of 80 m diameter (0.5 ha); 3. Gap-cutting (G): a circular gap in the closed stand (20 m diameter, approx. one height/diameter ratio); 4. Preparation cutting (P): 30% of the total basal area of the upper canopy trees and the whole secondary tree layer were cut in a circle of 80 m diameter; 5. Retention tree group (R): a circular group of upper canopy trees (20 m diameter, 8-12 dominant individuals, untouched sub-canopy layer) was retained in the clear-cutting. Control, clear-cutting, retention tree group and preparation cutting represent characteristic stages of the rotation forestry system, while gap-cutting is often implemented in the framework of continuous cover forestry (selection forestry system). The treatments were established during the winter of 2014/2015. The resulting 30 plots (5 treatments \times 6 blocks as replicate) were treated as basic sampling units.

The microclimate and soil conditions have been continuously monitored as a part of the project (Kovács et al. 2018, 2020). After the first three years, clear-cuts were characterized by increased mean and variability of air and soil temperatures. Retention tree groups could effectively ameliorate the temperature extremes but not the means. Preparation cuts induced slight changes from the original buffered forest microclimate. Despite the substantially more incoming light, gaps could keep the cool and humid air conditions and showed the highest increase in soil moisture after the interventions.

Data collection

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

Analyses

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

In the taxonomical approach, the effect of treatments on species composition was explored by Principal Component Analysis (PCA) with a square-root transformation for investigating the separation of treatments in different years, as well as the relationships between species composition and treatments (Venables & Ripley 2002). The separation of the treatments was statistically tested by Permutational Multivariate Analysis of Variance (PERMANOVA) using Euclidean distance (Anderson 2001). The species associations to treatments were confirmed by the Indicator Value Analysis (IndVal) method (Dufrêne & Legendre 1997). We considered a species as characteristic for a particular treatment type when both the ordination (PCA) and IndVal revealed their association to that treatment. All of the analyses of species composition (PCA, PERMANOVA, IndVal) were carried out for each year separately.

During the evaluation of the functional approach, traits related to body size, wing morphology, breeding season, overwintering stage, feeding preference and habitat affinity were collected for each species (Appendix S1: Table S1 in Elek et al. 2022) using the available literature (Thiele 1977, Lindroth 1985, 1986, Larochelle 1990, Hürka 1996, Turin et al. 2003). The final list of the assessed functional traits was habitat preference (forest specialists, open-habitat species and generalists), wing morphology (brachypterous, macropterous) and feeding preference (carnivores, omnivores) due to data saturation. These functional differences between species in a community cannot be described quantitatively by traditional diversity measures (e.g., Botta-Dukát 2005). Several functional diversity indices are available, the most common measures assume that within- and between-group differences are equal and ignore the abundance of the characterized group (Mason et al. 2003, Botta-Dukát 2018). Botta-Dukát (2005) proposed an index (FDQ or Rao's Q) based on the quadratic entropy of Rao (1982), which considers the relative abundances of the species and measures the pairwise functional differences between species. One of the major advantages of Rao's Q is that it can handle the species abundances and many traits (Loreau 2001, Botta-Dukát 2018), thus we applied this index to characterize the functional diversity for management types and years. We built Generalized Linear Mixed Models (GLMMs) to separate the effect of the two analytical foci. The effect of treatments and years and their interaction (considered as fixed effect terms) were tested on the set of response variables, while blocks were used as a random factor to consider the spatial replicates. In GLMMs, as response variables, species richness and abundance per plot were used in the taxonomical approach, while the calculated Rao's Q values and the abundance of selected functional groups were considered in the functional approach. Two distribution families, "Poisson" and "Gaussian", were applied to ensure the best fit of the tested data on abundance at all measures and on expected values of species richness and functional diversity by Rao's Q, respectively. The models were tested with the default Laplace approximation to the log-likelihood.

The model diagnostics include the inspection of model residuals' structure (Pearson's type) versus fitted values and degrees of freedom either in the model's output or in graphs. In case of significant treatment effects, the differences between treatment levels were evaluated by pairwise multiple comparisons with Tukey computed contrast matrices .

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

Results

Assemblage composition and species-treatment associations

The PCA analyses revealed that after the implementation of treatment types in early 2015, the carabid assemblages occupying the retention tree groups and clear-cuts formed a distinct group, while other treatments formed another one; a similar trend was revealed in 2016. The control plots became distinct from all other treatment types in 2017 and 2018 (Fig. 3.1.2). The greatest separation between the treatments was found in the third year (2017) of the experiment. The species associated with the studied treatments showed treatment-specific variation between years (Table in Fig. 3.1.2); *Aptinus bombarda* was associated with control forests in all studied years, *Abax ater* and *Carabus hortensis* were also control-associated species but only in 2016. In the clear-cuts, *Pseudophonus rufipes* and *Carabus granulatus* were characteristic species in the first two years of the study (2015-16), while *Carabus coriaceus* was the only species associated with clear-cuts in 2017. In 2018, *Pterostichus melanarius* and *Carabus scheidleri* became associated with clear-cuts. *Nebria brevicollis* was associated with gaps in 2015, while in 2017 it was *A. ater*, *Carabus convexus* was characteristic species for retention tree groups in the first two years of the study; while *Calathus fuscipes* became associated with this treatment in 2016 and 2017. *Laemostenus terricola* and *Notiophilus rufipes* were also characteristic for retention tree groups in 2015 and 2017 respectively. *C. coriaceus* in 2016, while *Carabus nemoralis* in 2017 were the species associated with preparation cuts.

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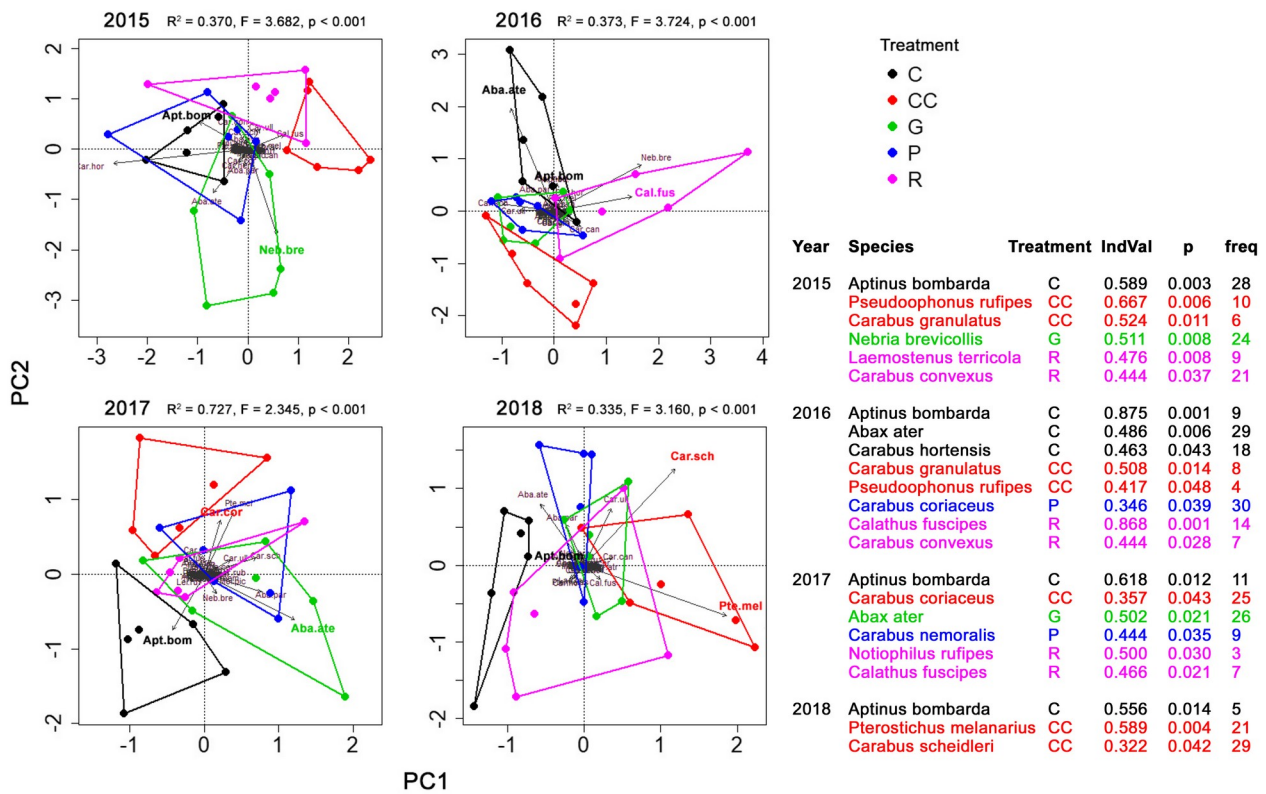


Figure 3.1.2 Biplots of the PCA on the abundance of the ground beetles. The compositional difference between treatments expressed as the results of the PERMANOVA (R^2 – coefficient of determination, F and p values) are portrayed on each graph panel. The table on the right summarizes the maximal indicator values of species and their significance to treatments based on the IndVal method. Only significant results ($p < 0.05$) are shown. The treatments are control (C, black), clear-cutting (CC, red), gap-cutting (G, green), preparation cutting (P, blue) and retention tree group (R, purple).

Species richness and abundance

The overall species richness and abundance of carabids decreased in the consecutive years; treatment effect revealed a year-specific change for both measures (Table 3.1.1; Fig. 3.1.3). For species richness, the effect of treatments was modest and had a significant effect only in 2016. This year, it was the highest in the retention tree groups and the lowest in the clear-cuts; other treatments had intermediate positions. For abundance, an immediate mass effect was revealed after the implementation of treatment types. In 2015, most individuals occurred in preparation cuts, control and gap cuts, and the retention tree groups and clear-cuts hosted the fewest individuals. Later, the patterns became inconsistent: in 2016, the control and retention tree groups had the highest, while in 2018 the lowest abundance values.

Table 3.1.1 Summary of the generalized mixed effects models for all studied response variables of ground beetle assemblages in the Pilis Mountains, Hungary. Significant effects are in bold and Tukey multiple comparisons for treatment types and years are designated by relation signals, where the “≥” designate the subsetting or partial differences among treatment types. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P) and retention tree group (R). Significance is marked by bold.

Group	Variables	χ^2	df	p	Comparisons
Species richness (Gaussian)	treatment	16.778	4	0.002	R>CC
	year	141.568	3	< 0.001	2015>2016>2017=2018
	treatment:year	20.962	12	0.051	
Abundance (N) (Poisson)	treatment	320.62	4	< 0.001	P=G>R=C>CC
	year	7663.91	3	< 0.001	2015>2016>2018>2017
	treatment:year	438.77	12	< 0.001	
Functional diversity, Rao's Q (Gaussian)	treatment	61.984	4	< 0.001	CC>P=C, CC>G, R>P=C
	year	53.768	3	< 0.001	2017>2015, 2017>2018
	treatment:year	15.133	12	0.234	
Forest species (N) (Poisson)	treatment	1064.26	4	< 0.001	C>G, C>R, C>CC
	year	7750.17	3	< 0.001	2015>2016>2018>2017
	treatment:year	137.19	12	< 0.001	
Generalists (N) (Poisson)	treatment	220.54	4	< 0.001	CC>R=G=P>C
	year	811.68	3	< 0.001	2015=2016>2018>2017
	treatment:year	278.65	12	< 0.001	
Open-habitat species (N) (Poisson)	treatment	371.478	4	< 0.001	R>CC>P=G=C
	year	216.163	3	< 0.001	2015>2016>2017=2018
	treatment:year	60.844	12	< 0.001	2016
Brachypterous species (N) (Poisson)	treatment	395.56	4	< 0.001	P>G, P>C, P>R, P>CC, G>R, G=C>CC
	year	7222.03	3	< 0.001	2015>2016>2018>2017
	treatment:year	411.96	12	< 0.001	
Macropterous species (N) (Poisson)	treatment	277.63	4	< 0.001	R>C, R>P, G>C, G>P
	year	555.46	3	< 0.001	2015>2016>2017>2018
	treatment:year	321.29	12	< 0.001	
Carnivores (N) (Poisson)	treatment	595.57	4	< 0.001	P≥G≥C>R>CC
	year	7863.2	3	< 0.001	2015>2017
	treatment:year	260.18	12	< 0.001	2015
Omnivores (N) (Poisson)	treatment	400.917	4	< 0.001	CC=R>P=G>C
	year	56.231	3	< 0.001	2015>2017
	treatment:year	224.495	12	< 0.001	

Functional diversity and functional group responses

For functional diversity (Rao's Q), the effect of treatments and years had a similar influence. In all years, it was the highest in the clear-cuts and retention tree groups (Table 3.1.1; Fig. 3.1.3). When species were grouped by their habitat affinity types, there was a strong treatment and between-year variation, suggesting the overall decline of carabids during the years (Table 3.1.1; Fig. 3.1.4). The

abundance of forest species was the highest in the control, intermediate in gap and preparation cutting and the lowest in clear-cutting and retention tree group but only in the first two years. The treatment differences decreased in 2017 and 2018. The abundance of generalists was consistently higher in all treatments than in the control. The abundance of open-habitat species was the highest in the retention tree groups, followed by the clear-cuts and preparation cuts, while open-habitat species were the least abundant in the gaps and the controls.

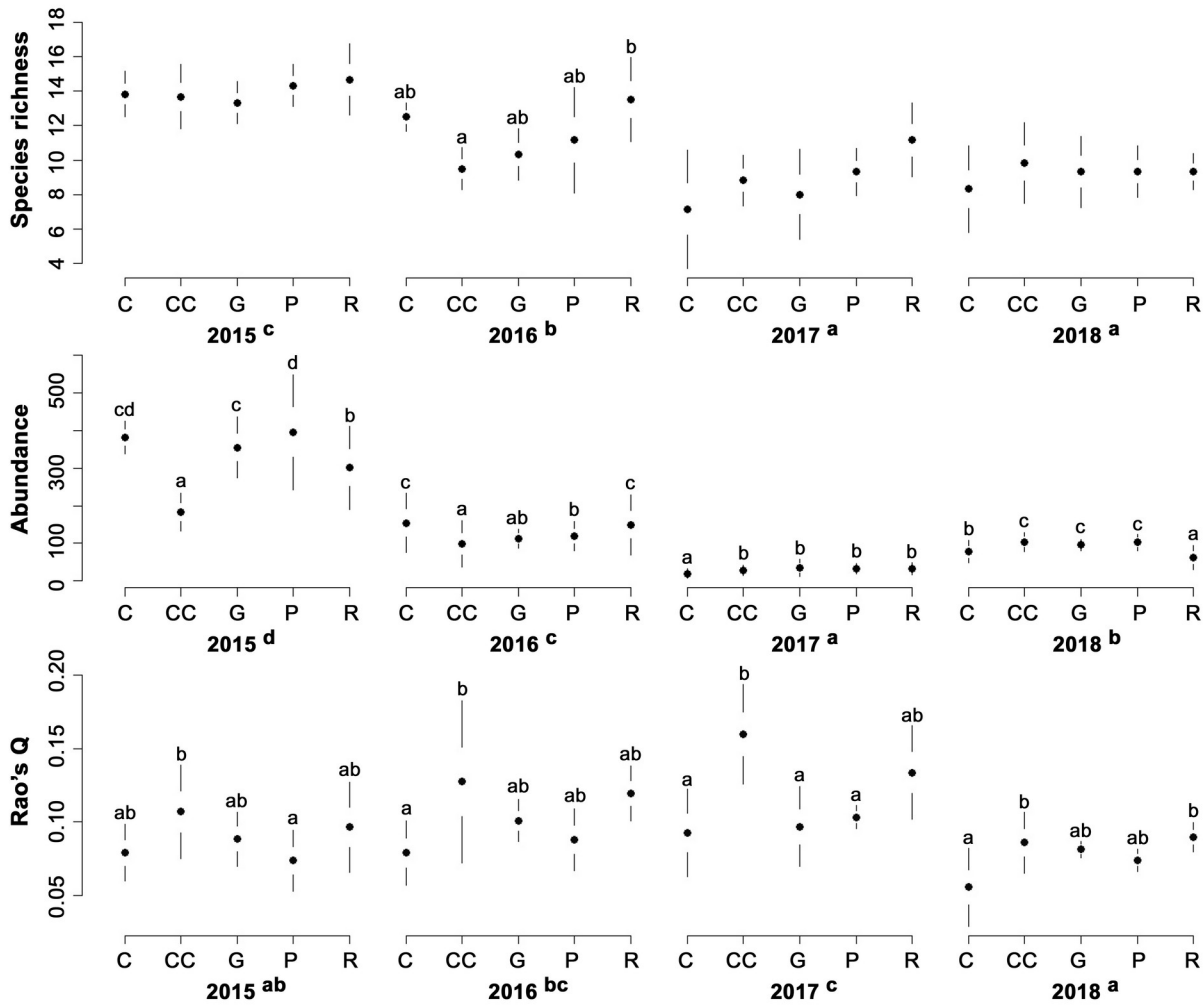


Figure 3.1.3 Response of carabids' species richness, abundance and Rao's *Q* to forestry treatments and years. Full circles show the mean, white space between the circles the standard errors of the mean, while vertical lines denote the standard deviations. The letters designate significant differences among treatments and years; the significance level was set at 0.05. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P) and retention tree group (R).

The wing morphology types showed contrasting responses for the various treatments (Table 3.1.1; Fig. 3.1.5). Brachypterous species were the most abundant in preparation cuts and controls followed by gaps and retention tree groups, while clear-cuts had the lowest abundance for this group. This trend was the most evident in 2015 and became less distinct over the years. Macropterous species

were most abundant in the gaps in 2015, in retention tree groups in 2016, while no considerable differences among the treatments were found in the last two years.

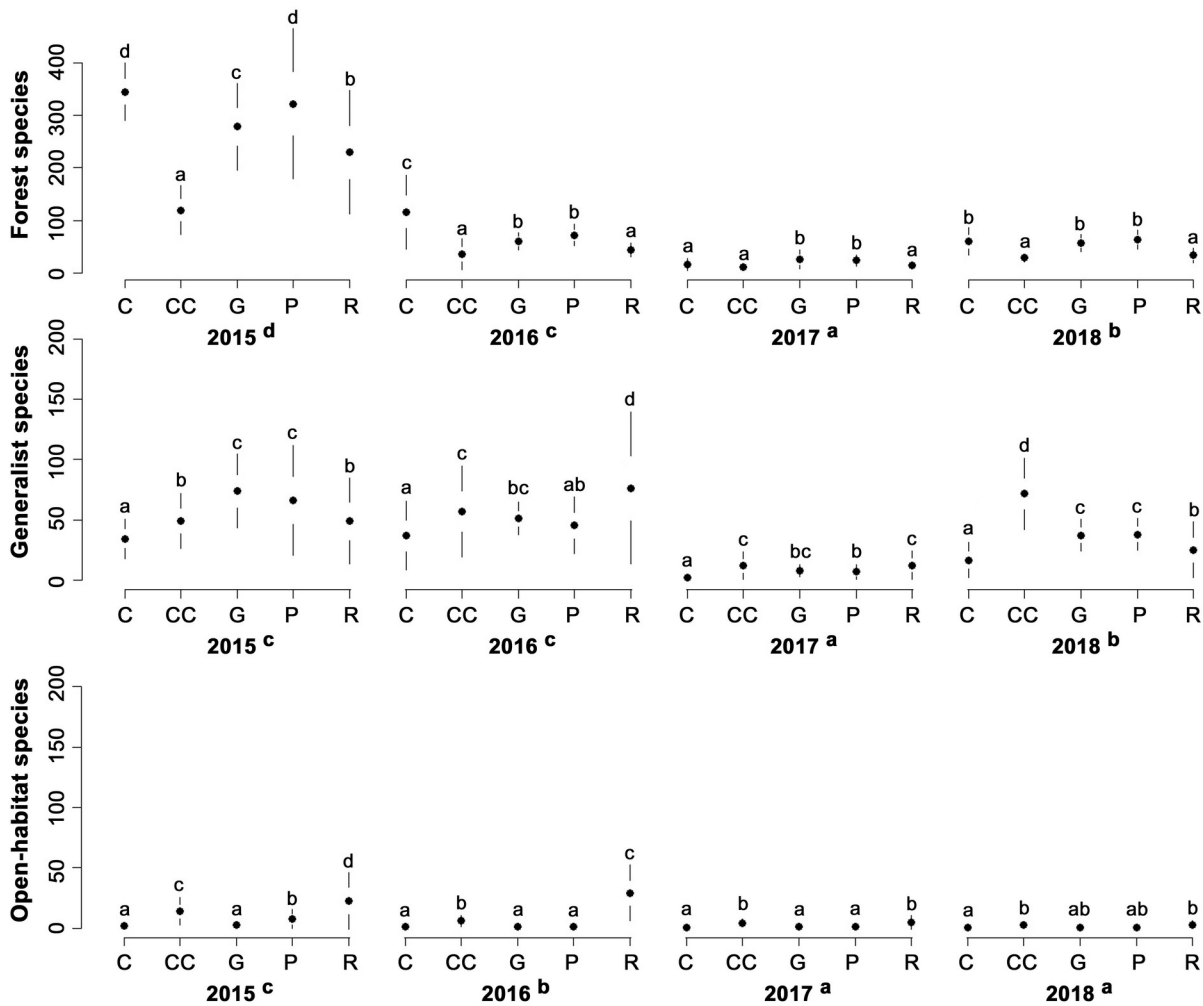


Figure 3.1.4 Response of activity density of carabids' habitat affinity groups to forestry treatments and years. Full circles show the mean, white space between the circles the standard errors of the mean, while vertical lines denote the standard deviations. The letters designate significant differences among treatments and years; the significance level was set at 0.05. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P) and retention tree group (R).

The assemblages, when sorted on the basis of feeding habits, showed similar responses as in the case of wing morphology (Table 3.1.1; Fig. 3.1.5). The abundance pattern of carnivorous species was the same as those of the brachypterous species, suggesting the preference towards more closed habitats such as gaps, preparation cuts and controls (Table 3.1.1). The omnivorous species showed the opposite trend and were the most abundant in more open habitats such as retention tree groups and clear-cuts.

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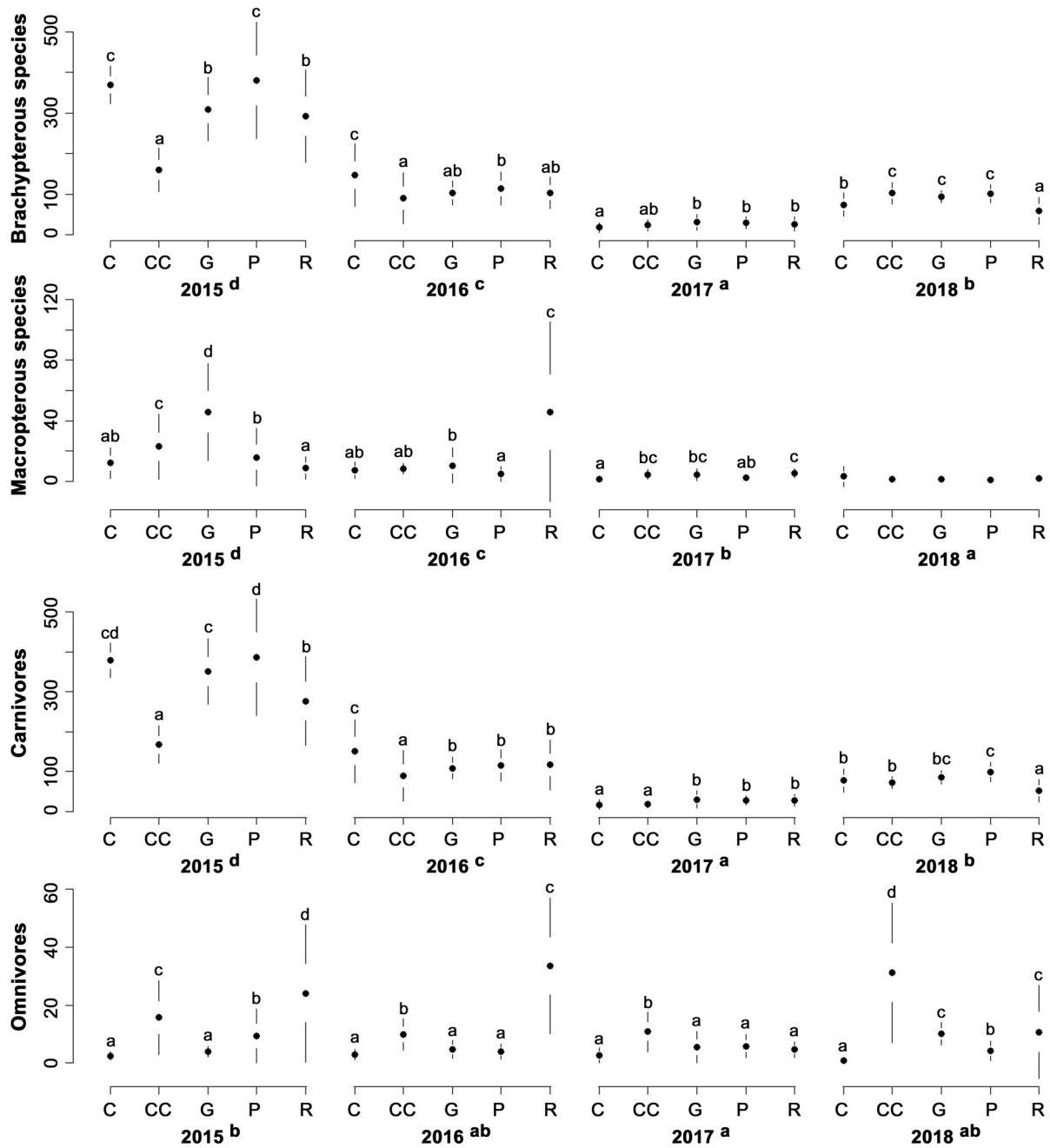


Figure 3.1.5 Response of activity density of carabids' wing morphology and feeding preference types to various forestry treatments and years. Full circles show the mean, white space between the circles the standard errors of the mean, while vertical lines denote the standard deviations. The letters designate significant differences among treatments and years; significance level was set at 0.05. The treatments are control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P), retention tree group (R).

Discussion

Clear-cutting and retention tree group had the most profound effects on carabid assemblages, either on the basis of taxonomical or functional characteristics. There is a high functional diversity characterized by mostly omnivorous, open-habitat and generalist species within these treatments. The opposite patterns were detected in more closed habitats (control, gap- and preparation cutting) characterized by low functional diversity with the high abundance of forest species and carnivores. These congruencies between functional responses can underline the fact that species traits can shape the assemblage composition, especially in the medium-term responses for forestry treatments.

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

Species composition showed high variation between years and treatments, the major finding was that the closed, control forest remained distinct from all other treatments over the four years suggesting that the recovery of carabid assemblages has not yet started. This is congruent with Koivula et al. (2019), where the carabid assemblages remained different after 10 years of the forestry intervention. The considerable differences in species composition between treatments and years suggests that seasonal variation in activity can appear even in closed forests, as in our study (Heikala et al. 2016, Pinzon et al. 2016, Koivula et al. 2019). This pattern can be explained by the fact that carabid assemblages in the early successional stage may have a long-term founder effect that governs the future assembly composition (*sensu* Weslien et al. 2011, Heikkala et al. 2016). In addition, the carabid assemblage composition of mature forests (i.e., control) can be strongly influenced by the long-term forestry and land-use history resulting in the decline of forest specialists in the forested landscape (Magura 2017, Elek et al. 2018, Koivula et al. 2019).

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

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

for carabids, whilst Pinzon et al. (2016) for spiders, found similar patterns in boreal forests after 10 years of forestry treatments. In addition, our findings also support the hypothesis that carabid assemblages were randomly organized from the original forest carabid species pool and the newly colonizing open-habitat and generalist species. Omnivorous species were more abundant in the clear-cuts and retention tree groups together with carnivorous species of moderate abundance. Heikkala et al. (2016) have found comparable responses, where the complex assessment of saproxylophagous beetles showed similar functional trait patterns in clear-cuts, suggesting that there is no clear resource utilization in more open habitat types. Similar patterns were also detected for dispersal ability: the abundance of brachypterous species was higher in the more closed habitats (control and preparation cuts) in the first two years of the study, whilst the abundance of macropterous species was inconsistent showing a random arrival of carabids to the more open habitat in the first two years. These patterns can be explained by the presence of dimorphic species where wingless (brachypterous) and winged (macropterous) forms can co-occur. The winged form of these species has higher colonization ability and can arrive in the early stages of succession (Kotze & O'Hara 2003), while the wingless individuals can support the assemblage persistence under stable habitat conditions (Elek et al. 2010, Nolte et al. 2017). This is congruent with the low functional diversity in control plots (i.e., closed forests), suggesting that the available functional space, in terms of the ecological niche concept, is already held mainly by carnivorous forest specialist carabids with low dispersal capacity (Nolte et al. 2017). The relatively homogeneous forest stand with closed canopy can prevent the establishment of more opportunistic carabids and ensure the persistence of forest specialists, which provides the functional stability of forest ecosystems (Sitzia et al. 2017).

3.2 Individual decisions drive the changes in movement patterns of ground beetles between forestry management types

The previous study (see Chapter 3.1) revealed that ground beetles, a group with moderate mobility, gave a weaker and somewhat less specific response manifesting in a general decline in abundance among several forest management types (Elek et al. 2018, 2022). This is presumably caused by the short-term response, which is explained by the loss of forest specialists due to forestry treatments (Niemelä et al. 2007, Elek et al. 2018). The large forest ground beetle, *Carabus coriaceus* (L. 1758), sensitively reacts to forest management and it is predominantly associated with the uneven-aged (mostly beech) forest stands (du Bus de Warnaffe & Lebrun 2004). This species is considered as a forest specialist with constant occurrence and abundance in the oak-hornbeam zone of the Pilis Mountains (Andorkó & Kádár 2006). *C. coriaceus* reproduces in autumn and overwintering as both larvae and adult, with the highest activity in the autumn (Andorkó & Kádár 2006).

The focus of forest ecology studies is at supra-individual level (Paillet et al. 2018) with their inevitable time constraints: the effects on populations and assemblages need several generations to unfold (Niemelä et al. 2007, Elek et al. 2022). Nevertheless, organisms can react to changing conditions in their habitats at lower organizational (individual or population) levels, including behavioural characteristics which are more immediate (Parsons 1992). Although animal movement is one of the most rapid responses to environmental changes, movement studies on insect are less numerous than that of vertebrates, and the majority of the published radio-telemetry studies on insects focus on methodological issues (Kissling et al. 2014). Only a few go further and study the movement characteristics over the total distance taken by the individuals (Negro et al. 2008, 2014, Růžičková & Vesely 2016). However, these studies did not quantify the distribution of the trajectory parameters such as step lengths and turning angles. Hitherto, there is a need for inferential methods that attempt to unravel relationships between factors driving movement, and predict them in quantitative terms. Hidden Markov models (HMMs) form a class of statistical models that have rapidly gained prominence in movement ecology due to the fact that they are able to adapt complex structures that account for changes between unobservable systematic states in movement (McClintock et al. 2020).

This study has aimed to explore and quantify the relationship between movement parameters and forest management types for ground beetle, *C. coriaceus* in a temperate managed oak-hornbeam forests in Hungary. Radio telemetry was used to record the average speed of movement and time when beetles were active and trajectory profiles in different forestry treatments, such as preparation

cuts and clear-cuts, and their control plots. In addition, it is crucial to decrypt distinct movement stages from trajectories and estimate their variation between individuals and treatments.

Materials and methods

Site description and study design

Our study plots belonged to the Pilis Forestry Systems Experiment

(<https://piliskiserlet.ecolres.hu/en/node/1>), which studies the effect of different forestry treatments on forest site, biodiversity and regeneration (further details are available in chapter 3.1 and Elek et al. 2018). Two of the four treatment types, representing characteristic stages of the rotation forestry system, were used for radio-tracking of ground beetles: 1. Clear-cutting (CC): a 0.5 ha circular clear-cutting area of 80 m diameter, surrounded by closed canopy stand; 2. Preparation cutting (P): 30% of the total basal area of the dominant tree layer and the whole secondary tree layer was removed in a spatially uniform way in a circle of 80 m diameter.

Radio-tracking of ground beetles

Six individuals (three males and three females) of the flightless *C. coriaceus* were collected in the study area by unbaited pitfall traps and mounted with “PicoPip” VHF radio tags (Biotrack Ltd., Wareham, UK). The maximum weight of the tags was 0.29 g with the individual frequencies between 150.325–150.915 MHz and the battery (type Ag 337) life-span of 8 days. Tags were fixed on the top of the beetles’elytra by cyanoacrylate glue (Loctite PowerFlex gel) with the antenna (5 cm) directed backwards (Fig. 3.2.1). Although Negro et al. (2008, 2017) revealed that this adhesive was more appropriate than the silicone gel (Riecken & Raths 1996), this gel was used for sealing the joint and make it waterproof. Individuals were kept for 24 hours in a dark box before their release and were fed ad libitum. Two of the tagged beetles were released in the centres of the treatments (CC or P), two at their edges and the last two in the adjacent control forest stand (C). Each beetle’s movement was tracked every four hours for five days in autumn 2018. During the experiment, we recorded the movement parameters for each beetle including their exact geolocation (hereafter, “fix”) by a GPS device (Garmin Dakota 20, in WGS84 coordinate reference system) and the absolute turning angle (i.e., angle towards a fixed point, such as magnetic north) and the distance from the previous location to correct potential GPS error. Fixes with the observed movement were considered active, while the fixes without activity as passive. The proportion of the

active time was calculated as a ratio between active and passive fixes. For each beetle and relocation, we also recorded the ground- and air temperature (in Celsius degree), relative humidity (as percent) and air pressure (in mmHg) with an automated loggers (Basetech 1065H, Conrad Electronic SE, Germany) as potential abiotic covariates with the exact date (year, month, day, hour, minute), that may influence beetles' activity (e.g., Thiele et al. 1977, Negro et al. 2017).

We further investigated the potential effect of the tag weights on beetles, and found that body/tag mass ratio was 14% on average, which is far below compared to previous findings for the same species (50% in Riecken & Raths 1996). Although tags can influence diverse aspects of a beetle's performance and such impacts remain understudied (Batsleer et al. 2020). We assumed that tags used in this study did not bias beetles' movement for the duration of individual tracking. Kissling et al. (2014), Růžičková & Veselý (2016, 2018) and Liégeois et al. (2016) proved that the consistency of the individual responses are not related to the samples sizes due to the individual behaviour of walking insects.

The target organism and forestry treatments were selected based on previous findings (Elek et al. 2018), where it was demonstrated that these treatment types had the most adverse effect on the assemblage composition of ground beetles. In the clear-cuts (CC), the loss of forest specialists was identified, including *C. coriaceus*, while the least adverse effects were detected in preparation cuts (P).

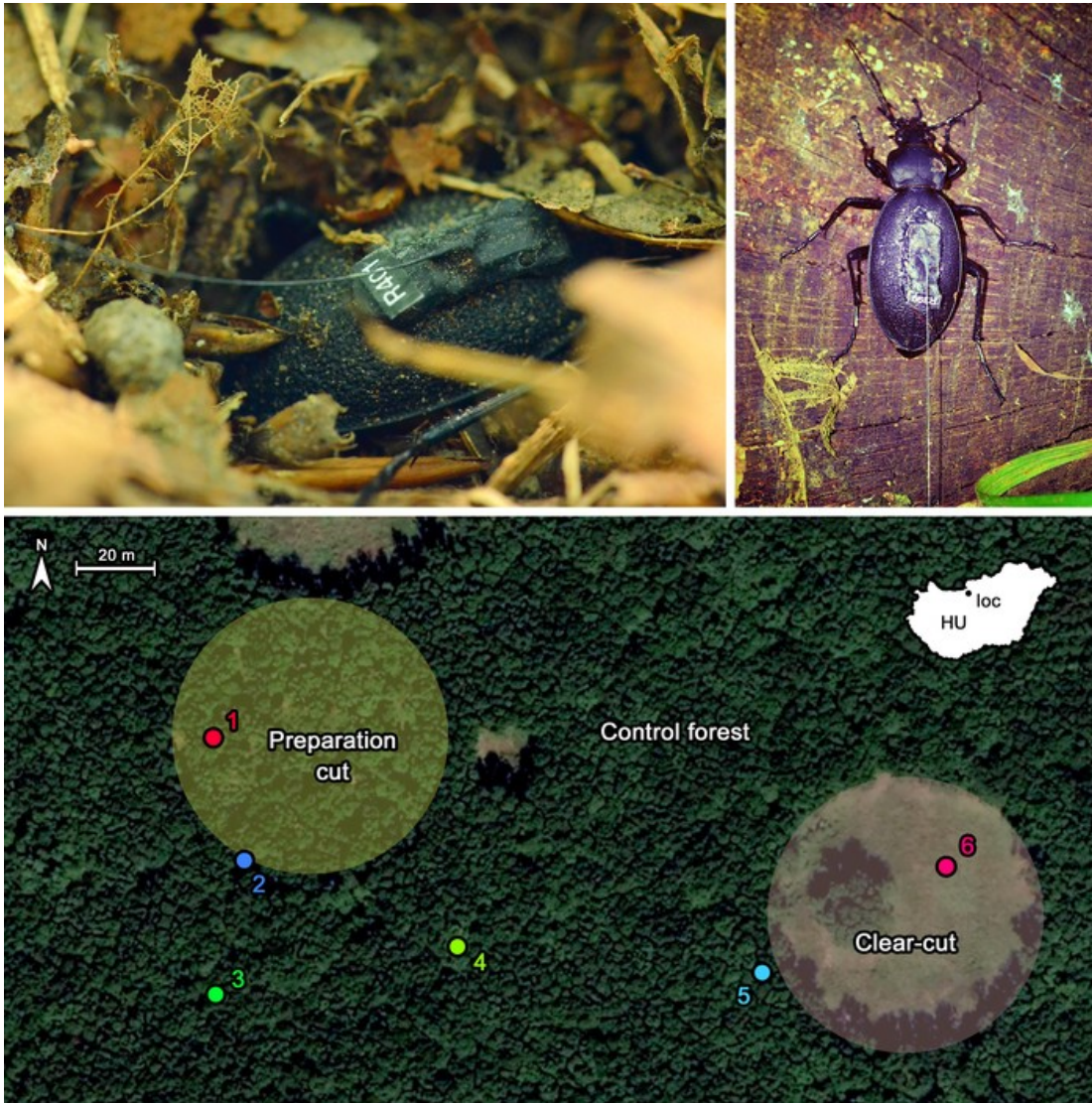


Figure 3.2.1 A tagged female of *Carabus coriaceus* (on the top right corner) and a relocated beetle (on the top left corner) with a radio tag hidden under the leaf litter and an aerial photo (on the bottom) about the study sites including the point of 1st release for each beetles Pilis Mountains, Hungary.

Data analysis

Although the statistical methods used in movement ecology are still evolving, the extensive analysis of movement data is still a challenge (Michelot et al. 2016, Patterson et al. 2017). Among the vast variety of models that have been used to analyze movement data, the Hidden Markov Models (HMMs) have a distinguished attention in recent years due to their appealing combination of model flexibility, clear interpretability and computational tractability (Michelot et al. 2016, Patterson et al. 2017). HMMs are part of an extended family of state-switching models focusing on the decomposition of the movement process into distinct underlying states. This approach matches our

intention to prove that most animals' movement is driven by switches in behavioural modes. In the models, two distinct stages of beetles' movement were identified based on the distance (as a step length in meters) and the direction (as a turning angle in degrees) between two movement steps in time: 1) Random walk is defined as the high proportion of (sharp) turns during the movement, the distance taken is relatively small (turning angles $>$ step length) and no explicit direction can be identified (Baars 1979, Kareiva & Shigesada 1983). The random walk is a good proxy for the foraging behaviour of animals (Thiele 1977, Kareiva & Shigesada 1983, Wallin & Ekbom 1988) indicating that the individual uses a habitat for living. 2) Directional movement can be described by the long distances taken between two movement steps with relatively flat turning angles and thus an explicit direction can be identified (turning angles $<$ step length, sensu Dray et al. 2010). This pattern is a neat proxy for migration from one habitat to another (Kareiva & Shigesada 1983, Wallin & Ekbom 1988). The applied HMM was based on a complete pooling, where all individuals were assumed to share the same movement parameters (Langrock et al. 2012). For modelling, the initial parameters of the step length (distances) with gamma distribution were set as $\mu = c(0.001, 0.01)$ for random walk (1 m limit \pm 0.11 m) and directional movement (10 m limit \pm 0.5 m), respectively; while the von Mises distribution was used to model the turning angles with initial parameters $\kappa = c(1, 1)$ for the same stages as above (Michelot et al. 2016) suggesting that turning angles have the same initial parameters for both states. All analyses were implemented in R 3.6.1 (R Core Team 2020) using the package *moveHMM* (Michelot et al. 2016) for trajectories.

Results

Movement characteristics of the individuals

During the experiment, we had 30 potential record slots (fix) for each individual due to the sampling protocol; however, the number of recorded fixes was within the range of 27–29 fixes, except for one male where the total number of fixes was 18. Therefore, we assumed that the collected number of fixes are adequate (more than 10 fixes/trajectory as suggested by Turchin et al. (1991) for further analyses (see details in Table 3.2.1). In addition, each individual has more passive fixes recorded than active ones. We found that the signal of beetle no. 4 (RP) has been lost at the end of the surveillance period (00:00 AM on 23/09/2018), due to predation likely by bats. Thus, the last step has been considered as biased, since we cannot exclude that this step is taken by the beetle itself or by its predator. Nevertheless, specimens showed much higher activities during the night than daytime. The correlation test for the movement parameters such as active step lengths, turning

angles and the most influential environmental variables revealed that the ground and air temperature are the most influential on the beetles' step length suggesting a decline in movement activity over 20°C (Fig. 3.2.2). However, this relationship can be biased by three outliers, thus we have tested the absolute differences in temperatures on step length and found no significant effect on movement (Fig. 3.2.2).

Table 3.2.1 Movement characteristics of the radio-tagged individuals of *C. coriaceus* in the Pilis Mountains, Hungary.

ID	Names	Sex	Treatment type	Locality	Mean speed (m/h)	Total distance (m)	Fixes active	Fixes passive	Total fixes
1	TMB	female	Preparation cut	treatment core	0.91	105.3	11	18	29
2	LG	female	Preparation cut	edge	0.32	35.9	4	24	28
3	MT	female	Preparation cut	control	0.19	22.9	4	25	29
4	RP	male	Clear cut	control	2.30	89.2	4	14	18
5	DM	male	Clear cut	edge	0.13	14.6	3	24	27
6	KH	male	Clear cut	treatment core	0.34	40.0	6	23	29

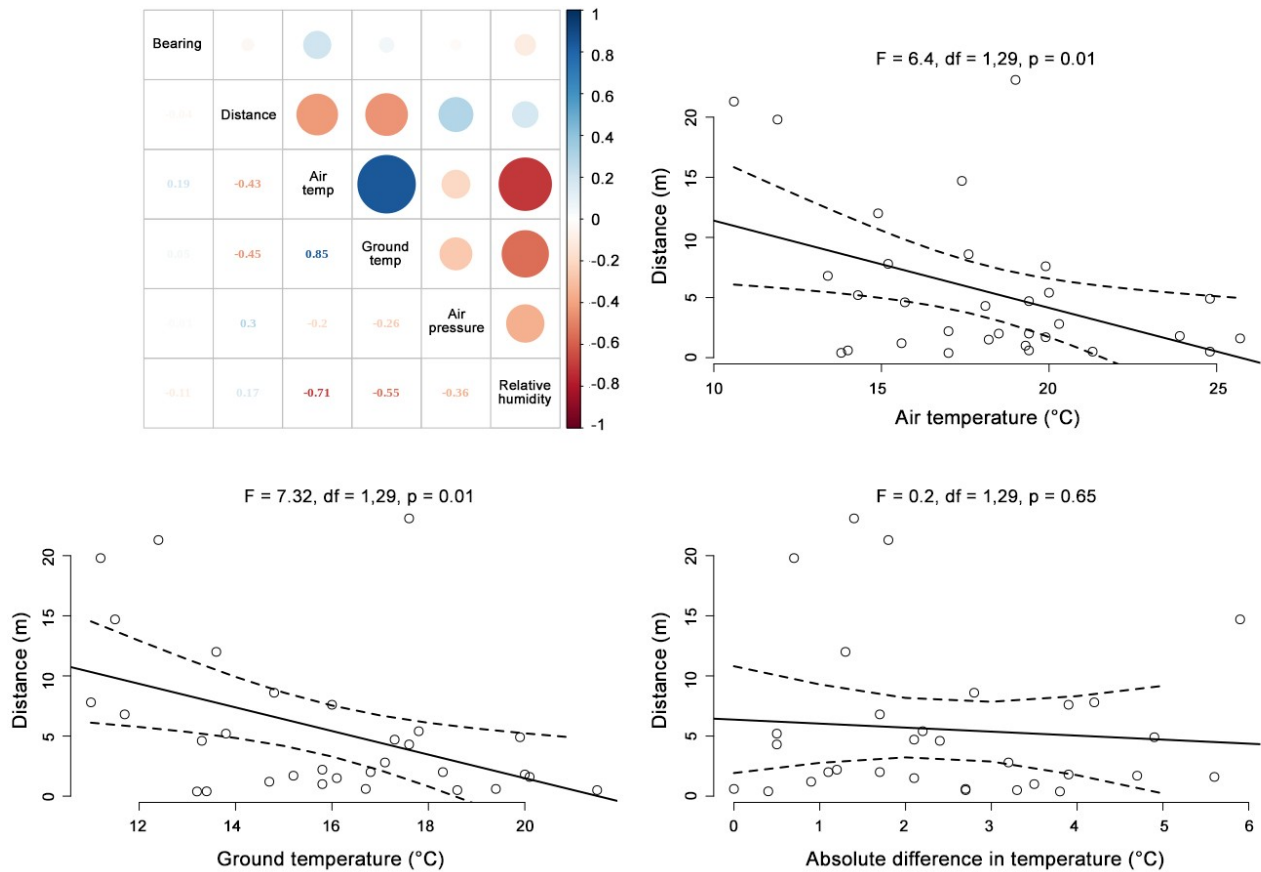


Figure 3.2.2 The overview of the Spearman's rank correlation test for exploring the relationship between movement parameters, step lengths (Distance, only active steps are considered) and turning angles (Degree) and the most influential environmental variables, air (T_a)- and ground temperature (T_g), air pressure and relative humidity of the air (RH). The effects of temperatures and their absolute differences ($T_a - T_g$) are visited on the separate graph panels; the 95% CI is based on the linear regression (output given on the top of each panel).

The complete pooling HMM gave the maximum log-likelihood, 34.773 with approximately normally distributed pseudo-residuals for the overall fit, thus the model parametrization was accurate. On average, the majority of step lengths were less than 10 meters, but 20- or 30 m-distances also occurred with the least frequency (Fig 3.2.3). The density of turning angles described well the two predefined movement states, negative turning angles (mean: -1.89 radians) were associated with random walk, while the positive turning angles (mean: 0.24 radians) were typical for directional movement. The transition probability for random to directional movement state (1→2) was 6.5%, while the probability for opposite state switching (2→1) was 90%. The proportion of the random walk and the directional movement for step length revealed that all movements were dominated by the random walk especially in the treatment cores (Fig. 3.2.3), while at the treatment edges and control, movements were dominated by high transition probability from the directional movement to the random walk. In addition, we also observed a consequent inactive phase in movement activities for 5–10 hours for all beetles. Both treatments were used only temporarily, and beetles were faster and more active there than in control forest (mean speed: 0.56 m/h in P, 0.33 m/h in CC, and 0.26 m/h in C; active time: 38% in P, 21% in CC and 18% in C).

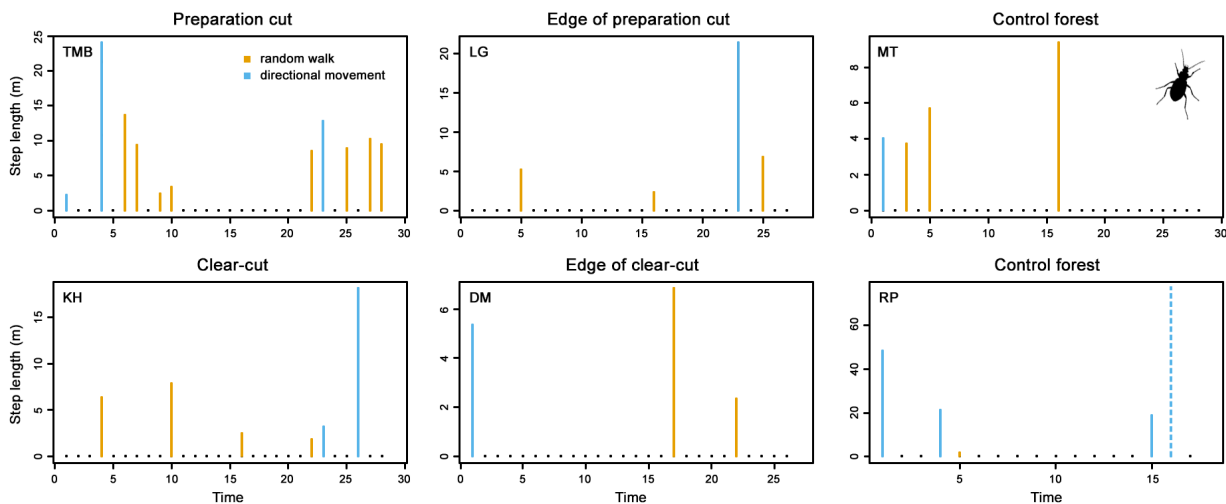


Figure 3.2.3 Distribution of active (bars) and passive (dots) steps and their length in time between forestry treatments. For beetle “RP”, the last detected step was considered as biased (movement after bat predation) and designated as a dashed line.

Moreover, they left preparation cuts, as well as clear-cuts within a few days. The profiles of each trajectory in both treatments were characterized by uneven angles and relatively long movement steps, indicating a definite walking direction toward the treatment edge, even though we observed the opposite pattern at the edges and control plots, where the random walk characterized the animals’ movement (Fig. 3.2.4).

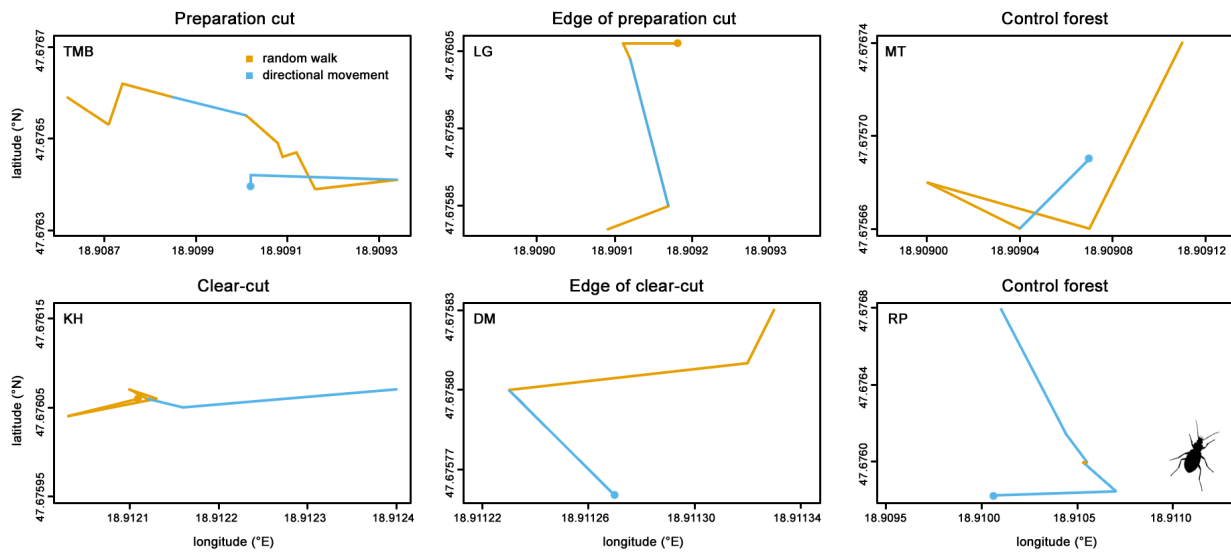


Figure 3.2.4 The individual trajectories of the studied specimens in different forestry treatments Pilis Mountains, Hungary. The yellow segments are designating the random walks, while the blues ones are for directional movements. For beetle “RP”, the last segment was considered as a biased one due to signal lost and designated as a dashed line.

Discussion

The study revealed that the radio-tagged beetles utilize the various forest management types regardless of the individual variation in movement. The two-state HMMs have given a quantitative assumption that clear-cuts are characterized by directional movement, while the random walk component was mostly used by the beetles in the more closed forest stands including preparation cuts, its edges as well as adjacent controls. This underlines the adverse effect of certain forestry treatments on animal behaviour, especially on movement patterns; the beetles escape from these sites after a few days of their release. In addition, we also observed that there is a no-movement phase in all trajectories that last for ca. quarter of a day.

Animal movement towards habitat use

For many arthropods including ground beetles, the soil surface, as a “groundspace”, provides habitat for a substantial part of their lives. It is essential for foraging, sheltering and migration (Vinatier et al. 2010, Hüppop et al. 2020). The groundspace is an acting scene for estimating the habitat utilization of ground-dwelling arthropods which is usually described by community-level

measures, such as activity density or species richness, found in a particular habitat type. The behavioural responses at the individual level provide more rapid feedback on the habitat use (Vinatier et al. 2010, Negro et al. 2017). There is a consensus that forest ground beetles tended to forage during the night (Thiele 1977), the results of this study also proved that the majority of active movement happened during the nighttime (Negro et al. 2008, 2017). It is an important clue, since the movement cannot be biased by the interference of daytime active forest-dwelling arthropods in the same habitat such as dung, rove and saproxylic beetles or spiders. This underlines the fact that there is a sophisticated spatio-temporal arrangement in functional traits in forest ecosystem to avoid density-dependent competition among species due to niche overlap (Didham et al. 1996). The frequency and the length of the active movement steps suggest that the individual have left the clear-cuts immediately and its trajectory can be characterized by a few long steps with definite direction toward the adjacent forest interior. This is similar to the findings of Negro et al. (2017) where the same pattern was detected for *C. olympiae* (Sella, 1855) in strip cuts (clear-cutting in a line) suggesting that forest carabids emerge from a habitat where the canopy has opened. Although the studied individuals have left the treatment cores quite quickly, the random walk was characterized by short and frequent movement steps in the preparation cuts assuming that foraging behaviour is more typical in thinned forests (Negro et al. 2008, 2017, Růžičková et al. 2021). In addition, the trajectory was similar to that in control forests suggesting that the still-closed canopy can be beneficial to keep forest specialist carabids in managed forest stand (Negro et al. 2008, 2017). Previous reviews (Brouwers & Newton 2009; Vinatier et al. 2010) revealed that only a limited number of studies are available on the movement characteristics of woodland arthropods. The straight-line movement rate was one of the first measures of insect movement in relation to body size (Lövei & Sunderland 1996). Large carabids, such as *C. coriaceus*, usually cover daily larger distances than smaller species likely due to their higher daily food requirement linked to their size (Lövei & Sunderland 1996, Riecken & Raths 1996). Nevertheless, the identification of species groups is often performed to develop generalizations about the ecological behaviour of invertebrates or lead to general recommendations in relation to conservation management (Lövei & Sunderland 1996, Brouwers & Newton 2009, Vinatier et al. 2010). Common approaches to categorize, mostly carabid, species include the degree of habitat specialization and physical traits, such as dispersal ability. Grouping ground beetles based on their mobility has been attempted in a long-term monitoring of heathlands in the Netherlands (Den Boer 1990a, b). This study revealed that this group was distinct in terms of dispersal ability and habitat occurrence (Den Boer 1990b). Heathland carabids could be categorized as species with low dispersal power inhabiting stable habitat vs. species with high power of dispersal inhabiting unstable habitat (Den Boer 1990a, b). In relation to

forest carabids, these categories can be equivalent to behaviour strategies in movement, such as migratory behaviour, which appears in altered habitat (i.e., open canopy layer in clear-cuts) whilst the random walk can be a proxy for designating stable habitats such as forest stands with closed canopy in preparation cuts and controls (Růžicková & Veselý 2016, 2018). In addition, this study underlines that trajectories in the treatment edges were not different from the control ones, suggesting that edges are so complex habitats and can be a lifeboat for forest specialists after forest management (Chiasson & Moreau 2020).

Movement vs. community measures

One of the most common measures for arthropod assemblages to estimate activity density is defined as the number of catches in relation to activity. Therefore, this measure can be considered as a reflection of animal movement, since the higher activity of the individuals will lead to the higher catches of those in a trap. Although this linear relationship seems evident at the first sight, movement attributes such as step length, frequency and turning angle can bias this correlation (Grüm 1971a, b). Our study proved an important behavioural aspect of carabids' movement, the individuals kept a quarter of the day lag in their movement regardless of utilized habitat types. A similar pattern was revealed for *C. coriaceus* in a previous study (Riecken & Raths 1996), where there was a 12-hour period of inactivity occurring regularly for all tagged individuals in grassland-forest strips in Germany. Previous studies (Ferrante et al. 2014, Fukuda & Konuma 2019) showed that carabids consist of a substantial part of the prey repertoire of several forest-dwelling birds and mammals. Therefore, any time lag in animal movement trajectories can act as direct evidence for the avoidance of native predators, although the predation pressure can be species-specific (*sensu lato* Eötvös et al. 2020).

3.3 Unequivocal differences in predation pressure on large carabid beetles between forestry treatments

Predation by various animals can be one of the most important drivers of carabid evolution and, together with abiotic factors, determines their activity patterns (Lövei & Sunderland 1996).

Although carabids have various morphological and chemical defense mechanisms to avoid or reduce predation risk (Brandmayr et al. 2009, Sugiura 2020, Giglio et al. 2021), they can also shift their behaviour in space and time to maximize their survival. As useful behavioural pattern, individuals can be active only in a certain part of the day or use different habitat patches than predators. Another option is to be hidden in the soil, under the leaf litter or understory vegetation. For instance, studies describing the activity patterns of some large carabid species reported relatively long periods of beetle inactivity between movements that can last even for a couple of days (Niehues et al. 1996, Riecken & Raths 1996). In some individuals, regardless of sex, this no-movement behaviour dominated the tracking period (Růžičková & Veselý 2018).

Although carabids are often studied as important natural enemies (Ferrante et al. 2014, Lövei & Ferrante 2017, Boetzl et al. 2020), they can also be predated due to their middle position in the food chain. In temperate forests of the Northern Hemisphere, carabids represent potential prey for a large spectrum of predators, including bats, hedgehogs, shrews, raccoon dogs, wild boars and frogs (Thiele 1997, Graclik & Wasielewski 2012, Fukuda & Konuma 2019, Suigura 2020,). Interactions between carabids and their predators might change due to shifts in the distribution of suitable habitat patches of various sizes within forest stands as a result of forest management (Negro et al. 2014, Elek et al. 2018, 2022). This is especially true for Europe, where the majority of temperate forests managed by rotation forestry (Bengtsson et al. 2000). Therefore, it is crucial to explore whether the spatial differences created by forestry practices can affect the predation pressure on carabids. In addition, it can be an important aspect to assess whether a certain treatment can act as an ecological trap for carabids (Ewers & Didham 2006), a habitat which is suitable for foraging or breeding, despite the fact that mortality can be higher there than in the unmanaged control forest stands.

There is an emerging need to estimate the structural changes in communities towards understanding ecosystem functions. Predation is well known as a key driver of these changes, potentially forming the community itself (i.e., keystone predation), and any change in predation intensity can reflect changes in ecosystem functions (Schneider et al. 2013). The technique involving artificial decoys as prey provides a powerful tool to assess relative rates of predation or predation pressure across various treatments (González-Gómez et al. 2006). Artificial prey is relatively cheap and easy to

manipulate, and it is not invasive as it does not involve living specimens (Belovsky et al. 1990, Pitt 1999, Bartholomew & Moghrabi 2018). This can be an important aspect, especially for rare or endangered species with low population densities where collection is nearly impossible (Fukuda & Konuma 2019). Using 3D-printed decoys seems to be more suitable than involving fragile dried specimens that can be easily damaged (Pearson 1985). Other frequently used materials, such as clay or plasticine (Ferrante et al. 2014, Sam et al. 2015, Lövei & Ferrante 2017), cannot replicate the narrow parts of beetles' body, such as legs and antennae (Fukuda & Konuma 2019). Yet, The sentinel prey method use these materials and techniques for modelling various invertebrates with simple body shapes, such as snails, slugs, caterpillars and earthworms (Ferrante et al. 2014, Howe et al. 2015).

In this project, there was experimentally tested the predation pressure on carabids in the Hungarian managed temperate forest using real-sized 3D-printed models as decoys. As a model organism for 3D decoys, a forest generalist, *Carabus coriaceus* (L., 1758), was selected as a large species commonly occurring in Hungarian oak–hornbeam forests that sensitively reacts to forestry practices (Elek et al. 2021, Růžičková et al. 2021). Two distinct types of forestry treatments, clear-cuts and preparation cuts, were used for the field experiment. They considerably differ from the surrounding unmanaged forest stands in terms of the height and cover of understory vegetation, the amount of leaf litter, the cover of bare soil as well as in microclimatic conditions (Kovács et al. 2018, 2020, Tinya et al. 2019). Hence, it was expected that the predation pressure will vary between forestry treatments and undisturbed control stands due to the different availability of shelters formed by dense ground vegetation or leaf litter. Moreover, the different activity patterns of potential predators may presume that the predation pressure will also have diurnal and seasonal aspects based on predator activity and breeding period. Based on these clues, the expected variation in the predation pressure was tested on large carabids at the different spatio-temporal scales. In particular, the study focused on microhabitat characteristics, habitat type and time to determine the most influential factor(s) of the predation pressure in the studied forest stands.

Materials and Methods

Study Area

The study was implemented as a part of the Pilis Forestry System Experiment (<https://piliskiserlet.ecolres.hu/en/node/1>) where four forestry treatments representing two different silvicultural systems were established in 2014. For the field experiment conducted in this study, two

of the four implemented treatments were used representing characteristic stages of the rotation forestry system: (1) Clear-cutting (CC) was a circular clear-felled area of 80 m diameter surrounded by a closed-canopy stand. (2) Preparation cutting (P) was created when 30% of the total basal area of the dominant tree layer and the whole secondary tree layer were removed in a spatially uniform way in a circle of 80 m diameter. These two treatments were chosen due to their contrasting effects on carabids at different levels, from community composition to individual activity (Elek et al. 2018, 2021, 2022).

Three-Dimensional Printed Decoys and Field Experiment

The 3D model of *Carabus coriaceus* was compiled in Blender 2.8 (<http://www.blender.org/>) based on high-resolution photos of real-sized individuals. One of the advantages of using this species is the large body size (33–40 mm), making the species suitable for detailed 3D printing. Unlike the other large species, *C. coriaceus* is unified in colour (black) without iridescence and it is one of the most abundant species in the area (Elek et al. 2022). The beetle model was converted into printing data by KISSlicer 1.6, and then life-size three-dimensional decoys were generated by the 3D printer (DeltiQ M, developed by TriLAB Group s.r.o., Brno, Czech Republic). Black polylactic acid (PLA) filament was used as a production material. The printed decoy was the same size as the real specimen (Figure 3.3.1a).

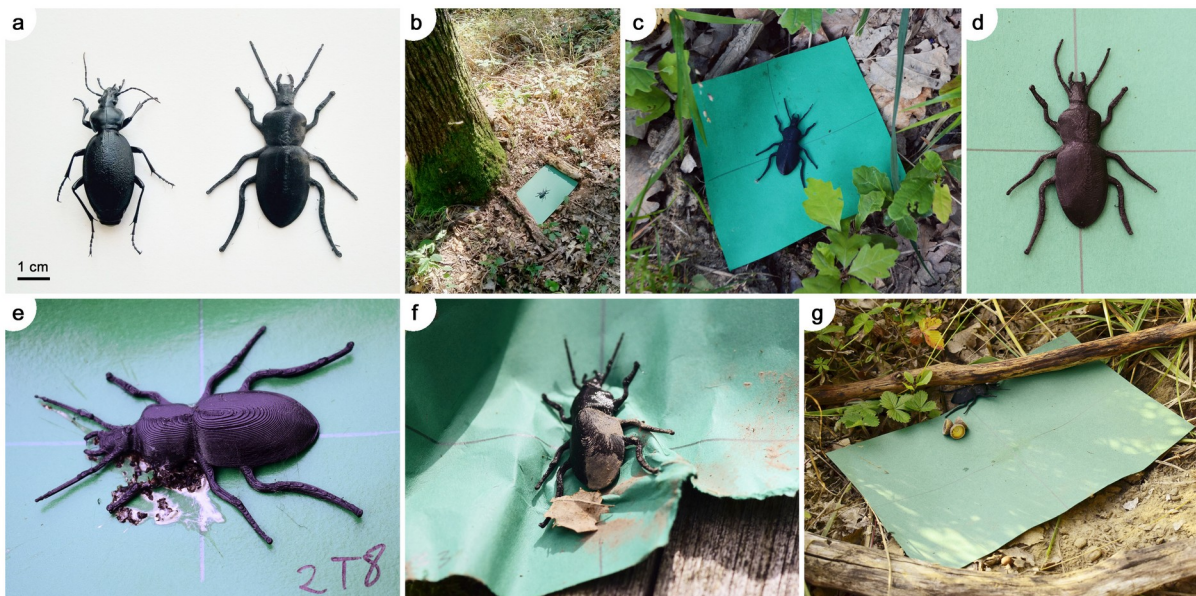


Figure 3.3.1 Printed decoy of *Carabus coriaceus* in comparison with a real individual (a). Decoys were installed on a green cardboard (b) for turns (c), broken or bent parts (d), predation attempts by birds (e), wild boars (f) or relocations (g).

The field experiment was conducted in two seasons, spring and autumn, which corresponded with the highest activity peaks of carabids in the area (Elek et al. 2018, 2022). In both treatments (CC and P) and control plots (C), we installed 10 decoys along two transects (each with five beetles) on the ground with an A5 cardboard sheet beneath them. Each plot (both treatments and control) was replicated in three blocks resulting in nine sampling plots. The distance between decoys was approximately 2.5 m. Decoys were positioned in the centre of the green-coloured sheet to avoid any unintended attraction due to conspicuous sheet colours (Figure 3.3.1b). The exact position was marked by two perpendicular lines drawn on the paper; the decoy was installed at their intersection to be able to record possible predation events. We recorded the cover of bare soil, litter, herbal and shrub layer (in %) in a one-meter radius circle around each decoy and the number of surrounding trees (see summary in Table 3.3.1). These environmental variables can potentially affect the distribution of carabids via the availability of shelters (Růžičková & Veselý 2018, Elek et al. 2021). In total, 90 *C. coriaceus* decoys were installed per season that were checked twice a day, in the morning and evening, for six consecutive days (7–12 September, 2020 and 8–13 June, 2021). The exposed decoy was considered attacked when it had been turned or moved/relocated from its original position, including its disappearance or damage, such as scratches, bites and missing parts. For turns, we measured the angle; if relocated, the distance was recorded. Although decoy turns suggest that the potential predator was interested in the exposed decoy, the relocation or scratches are clear signs of a predation attempt. After measurements, decoys were repositioned or replaced by new ones when was necessary.

Table 3.3.1: Environmental characteristics (mean values with standard error of the mean) of forestry treatments represented as the cover of bare soil, leaf litter, herb and shrub layers and the average number of trees per plot.

Treatment	Cover of (mean \pm SEM, in %)				No. of trees per plot (mean)
	Bare soil	Leaf litter	Herb layer	Shrub layer	
Control	2.51 \pm 0.52	68.70 \pm 2.68	28.25 \pm 2.59	0.58 \pm 0.37	4.67
Clear-cut	3.63 \pm 1.04	10.91 \pm 1.68	36.10 \pm 2.20	49.35 \pm 2.90	0.50
Preparation cut	4.11 \pm 0.97	33.36 \pm 2.39	50.40 \pm 2.76	12.10 \pm 2.14	2.67

Data Analyses

The predation pressure was considered as a ratio between attack and no-attack events on 10 decoys in a plot per measurement session. This response was coded as a two-column matrix [attack; no attack] in R 3.6.1 (R Core Team 2020) where all analyses were conducted. We used generalized linear models (the “glm” function of the *stats* package) with a binomial distribution and logit link function. Three different models were built considering various temporal and spatial scales. In the

first model, treatment (factor with three levels: control, preparation cuts, clear-cuts) was used as a single explanatory variable (spatial scale). In the second model, treatment, cover of leaf litter, bare soil and number of trees in the plot were included (micro-spatial scale). Cover of herbs and shrubs were excluded from the analyses due to a strong negative correlation with leaf litter (Pearson $r = -0.48$ for herb layer and $r = -0.70$ for shrubs). The treatment, daytime (factor with two levels: day and night) and season (factor with two levels: spring and autumn) factors were used in the third model (spatio-temporal scale). Then, using the `model.sel` function from the *MuMIn* package (Bartoń 2021), this set of models was tested to select the best model(s) based on information criterion corrected for small sample sizes (Akaike Information Criterion – AICc, Burnham & Anderson, 2002). The best model was selected as the most parsimonious explanation of the data when $\Delta\text{AICc} > 2$ for other models.

Table 3.3.2 Summary of the model selection; using estimations based on the calculated AICc value of the models, serving as the weight of evidence in favor of the different models. The most parsimonious model (delta < 2) is emphasized in bold.

Model	df	LogLik	AICc	ΔAICc	Weight
Spatio-temporal scale	5	-179.890	370.1	0.00	0.833
Spatial scale	3	-183.925	374.0	3.86	0.121
Micro-spatial scale	6	-181.705	375.9	5.77	0.046

Results

In total, 108 attack events were recorded based on 1800 observation events (i.e., the predation rate was 6%). Turn was the most common event in 87 cases, followed by scratches or broken parts in 13 cases and 8 relocations. The majority of turns were between 5° and 10° from the original position, and the maximal turn reached 45° . The mean distance for relocation was 11.8 cm and in one case the decoy was taken. Focusing on possible predators, bird droppings ($N = 2$) and wild boar hair ($N = 1$) on turned or scratched decoys were observed. Some of the recorded predation events are shown on Figure 3.3.1c–g.

The model selection showed that the “spatio-temporal scale” model was the best one, suggesting spatial and temporal constraints are the most influential explanatory variables on predation pressure (Table 3.3.2). Therefore, the predation pressure was significantly higher in both treatments than in the control forest (Table 3.3.3, Figure 3.3.2a). Moreover, the pressure was higher during the nights than daytime (Figure 3.3.2b). On the contrary, no effect of season or environmental variables was confirmed.

Table 3.3.3 The effects of treatment, daytime, season and environmental variables on the predation pressure. Significant effects are in bold, marginal in italics.

Model	Explanatory variables	χ^2	df	p
Spatio-temporal scale	treatment	11.334	2	0.003
	daytime	4.444	1	0.035
	<i>season</i>	3.625	1	0.056
Spatial scale	treatment	11.286	2	0.004
Micro-spatial scale	treatment	0.203	2	0.903
	leaf litter	0.973	1	0.323
	bare soil	2.404	1	0.121
	tree	0.010	1	0.918

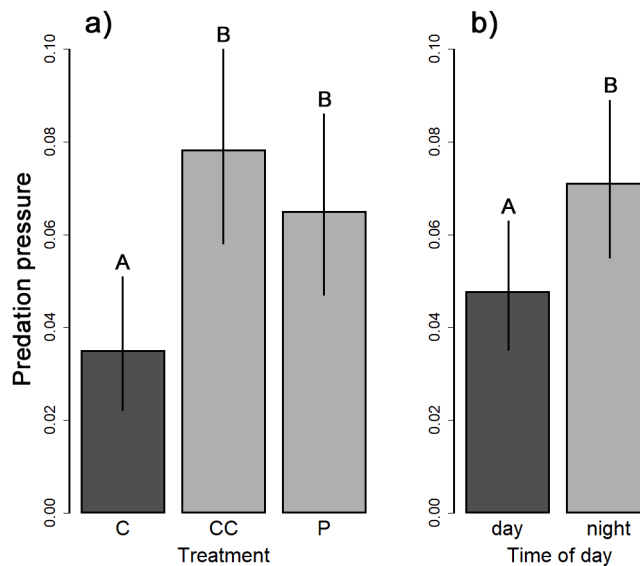


Figure 3.3.2 The effect of treatment (a) and time of day (b) on the predation pressure. Vertical lines represent a 95% confidence interval and different capital letters above the bars indicate significant differences based on Tukey multiple comparisons of means.

Discussion

It was revealed that 3D-printed decoys represent a suitable approach for testing predation pressure on large carabids since predators interacted with them. The predation pressure in the study area was affected by spatial and temporal constraints. More attack events were recorded in both treatments than in the control. Moreover, the predation pressure on the exposed carabid decoys was higher at night than during the daytime, and it did not correlate with any microhabitat features, such as leaf

litter or shrub cover, as they are not important for predators of large carabids. Taking into account the previous findings on habitat utilization by large carabids (Růžičková et al. 2021), both forestry treatments can act as an ecological trap for carabids, as these plots are used only temporarily and with a higher risk of mortality.

Although marks on decoys made from polylactic acid filament cannot deliver a detailed information about predator identity in comparison with plasticine models (Low et al. 2014), the decoys were eligible to determine some of the predators and suggest other possible candidates. The turn was the most common attack event occurring in most cases. Decoy turn may suggest an interest of the potential predator in the exposed decoy, investigating its edibility. Contrarily, scratches and relocations are clear signs of feeding attempts. Wild boar (*Sus scrofa* L., 1758) was determined directly, since we found its hair on one relocated decoy. Indeed, various carabid species were recorded as a part of the wild boar's diet (Schley & Roper 2003). From other mammalian predators, there was no direct evidence for attacking decoys, but their interest can be presumed as they commonly occur in oak–hornbeam forests of the Pilis Mountains. Eurasian badger (*Meles meles* L., 1758) is already known for feeding on carabids, including large ones, such as *C. coriaceus* (Fletcher 1992, Marassi & Biancardi 2002). Other potential predators could be the northern white-breasted hedgehog (*Erinaceus roumanicus* Martin, 1838) or the greater mouse-eared bat (*Myotis myotis* Borkhausen, 1797), which collect ground-dwelling insects directly from the ground, and large carabids were previously found in its droppings (Graclik & Wasielewski 2012). Moreover, bird droppings were recorded on two turned decoys. These droppings were found exclusively in the spring season, carabids may provide food not only for adult birds but also for nestlings. In addition, Eurasian nuthatch (*Sitta europaea* L., 1758) can feed its young with a high proportion of large carabid species, including the genera *Carabus*, *Calosoma* or *Pterostichus* (Thiele 1977).

The predation pressure was higher in the treatments than in the control undisturbed forest, thus the risk of beetles' mortality evidently increased after forest management/forestry practices. Some large carabids, including *C. coriaceus*, can penetrate clear cuts and preparation cuts in relatively high numbers, likely for foraging, since there is a high competition for the limited resources in the structurally homogeneous undisturbed forest (Růžičková et al. 2021). This kind of habitat utilization is rather transient, since individuals are able to leave the treatment sites within a couple of days (Elek et al. 2021; Růžičková et al. 2021). There is a high risk of predation in both treatments modified by forestry practices; therefore, these habitats may act as an ecological trap for carabids. The ecological trap is a habitat that is actively selected by individuals despite higher costs of utilization, due to increased mortality and low breeding success (Ewers & Didham 2006). Altered habitat patches are often mentioned as an example of an ecological trap for various animal groups,

including insects (Ries & Fagan 2003, Ewers & Didham 2006). The results of this experiment do not support the increasing disturbance hypothesis (Gray 1989), suggesting that predation pressure in modified habitats is lower than in undisturbed ones due to the declining number of predators (Eötvös et al. 2018, 2020). Treatments included in our study were, however, relatively small (with a diameter of 80 m) in comparison with landscape gradients and surrounded by undisturbed semi-natural forest. It can be assumed that large predators, such as wild boars, can easily move across plots regardless of disturbances.

Forestry treatments differ in terms of microclimatic conditions and the structure of understory vegetation from the control forest (Kovács et al. 2018, Tinya et al. 2019). Nevertheless, no effect was found of any environmental variable on the predation pressure. Microhabitat features, such as the cover of leaf litter or herbs, of a particular patch are important factors for the distribution of carabids (Niemelä et al. 1992b, Pearce et al. 2003, Wehnert & Wagner 2019), but not for their predators, as they move at larger scales and likely consider the same patch as structurally homogeneous. Additionally, the predation pressure was higher at night than in the daytime. This seems to be coherent with the fact that *C. coriaceus* is predominantly nocturnal (Riecken & Raths 1996, Elek et al. 2021) and most mammalian predators are more active during nights, which may result in an overlap in the activities of preys and potential predators. One of the options to avoid predators is to switch movement activity to the daytime when the predation pressure is lower. Indeed, beetles, previously considered as strictly nocturnal, were observed to be active during the daytime as well (see Riecken & Raths 1996 and Elek et al. 2021 for activity patterns of *C. coriaceus*). However, there is still a risk of diurnal predators, such as birds. Another option is to minimize the encounters with predators by being hidden as much as possible in shelters. Based on radio-tracking studies, large carabids are able to be inactive for a couple of days, hidden under leaf litter or burrowed in soil (Niehues et al. 1996, Riecken & Raths 1996, Růžičková & Veselý 2018). In *C. coriaceus*, this anti-predation behaviour was observed especially in closed (recently undisturbed) forest (Elek et al. 2021, Růžičková et al. 2021), where the high amount of leaf litter seems to be ideal to hide.

It is crucial to underline some methodological perspectives and limitations of using 3D-printed decoys for testing predation pressure. This approach is suitable for recording the exploratory behaviour of various predators, as they frequently interacted with decoys and turned them. Exact predator identification was, however, limited, as the used printing material (polylactic acid filament) is rather tough for recording soft and small bites. The use of softer and more elastic printing filament is not eligible for printing fine and detailed body parts, such as legs or antennas. The surface of 3D-printed decoys also could not mimic the structural colours of the real carabid cuticle,

especially if the model species has metallic iridescent colourization (Fukuda & Konuma 2019), and this may bias attractiveness for predators. In addition, there is a chance that the same animals might attack them, leading to an overestimation of predation pressure.

3.4 Conclusions

The work presented in this chapter demonstrated the following evidences:

- 1) The community-level measures such as species richness, abundance and diversity were more sensitive than functional traits to describe between-year variation and structural changes of beetle assemblages in time. However, the functional traits approach revealed that treatment-induced differences were more important than between-year variation. The simultaneous use of the two approaches will provide the most articulate understanding of the status of ground beetles assemblages in response to forest management and help to explore which group of ground beetle can be sensitive to disturbances.
- 2) The functional redundancy in clear-cuts and retention tree groups is related to the invasion of habitat generalist and open-habitat species with high dispersal power causing a decline in the population of true forest-dwelling carabids with weak dispersal ability. This functional difference remains consistent between years suggesting that the population of mostly carnivorous forest specialists with low dispersal power have not yet regenerated four years after the implementation of the studied forestry treatments.
- 3) It is still a common debate how to use animal movement in species conservation action plans. The findings above showed that there is a standard and quantitative way to analyse the insect movement suggesting that opening in forests can be a sink habitat for predominantly forest carabids and the surrounding closed stands are the key to the recolonization of the open areas by forest specialists. Hitherto, the regular time lag with no activity in trajectories can be a key driver for survival due to the avoidance of predators. This clue can be also a frontier to plan further studies toward predator-prey co-evolutionary adaptation based on individual movements.
- 4) The results revealed that the movement at the individual level cannot be directly connected with the community level, thus the generalization for effective conservation is rather unfolded. Therefore, there is a demand to explore and adapt the existing analytical tools in movement ecology including arthropods, even though the approach can be biased by spatial constraints of insect movement.
- 5) Although community measures are widely used, new facets appear and serve as a good proxy for ecosystem functioning including animal behaviour. The estimation of predation risk can reflect how

animals can select their habitat for foraging, breeding or overwintering. However, drawing such a conclusion, the knowledge of the spatio-temporal habitat use of beetles is required, suggesting that other methods should be employed alongside 3D-decoys, such as radio telemetry. Understanding how the interactions between prey and predators can change in modified habitats is crucial for better predictions of species-specific responses to habitat alteration.

6) Although the methodological aspects of insect behavioural ecology develop progressively in relation to equipment and statistical tools, the insect movement studies have still remained rather method-centred, only a few studies address any ecological issue being tested by telemetry. The radio telemetry and predation pressure studies revealed that habitats modified by forestry practices may act as an ecological trap for carabids.

4. Training-through-the-research: method-centred innovations

One of the most evident attributes of any kind of research is the reconsideration of the already known methods and approaches occasionally. Although the majority of the conceptual or methodological approaches can be widely utilized as it is in various fields of the research, in some occasions, there is a need to refine or reconsider the concept or methods to better suit better to the major motivation of the research. In this chapter, I will overview the methodological advances, inventions which was implemented during the above-mentioned research projects. In chapter 4.1 I will outline a simple, but effective graphical method to compare the seasonal activity of carabids in the urbanised woodlands, whilst in chapter 4.2. I will compare and critically review the two most common field methods to record animal movement on a fine spatial scale.

4.1 The use of percentile-percentile plots to compare differences in seasonal dynamics, illustrated by the case of ground beetles reacting to urbanisation

One rapidly changing parameter reflecting the behavioural change in response to environmental conditions (i.e., prey availability, habitat quality, disturbance regimes, etc.) is the seasonal activity. Environmental changes could trigger a delay in the start of the activity, or change the timing of activity peaks. Such reactions are faster than those in population parameters, and can thus signal environmental change earlier than population- or community-level parameters, provided reliable indicators of such reactions are available.

Data analysts (e.g., Cleveland 1993) emphasise the suitability of graphical data exploration methods in analysing scientific data. Such methods are simple and very useful to generate hypotheses for further analysis, yet are often neglected. A simple graphical technique to visualise the comparison of activity curves is the percentile-percentile plot (p-p plot) of Wilk & Gnanadeshikan (1968).

Apparently, this method has not been used in entomology or ecology (literature search on Web of Knowledge in January 2022, found no relevant articles). The method relies on the ability of the eye to detect and easily interpret even small deviations from the perfect diagonal line. This technique was used to examine the carabids database collected in the urbanisation research project, as reported in chapters 2.1 and 2.2.

During advancing urbanisation, ground beetle assemblages undergo a substantial rearrangement indicating a general decrease in habitat quality. However, species reactions are different: certain forest specialist species become rare or disappear, while other species only appear in the most urbanised habitats (Magura et al. 2010a,b). By the evaluation criteria so far applied in published

Globenet studies (species presence, total activity density over the season), generalist or ubiquitous species did not show significant trends in response to increasing disturbance as a result of urbanisation.

During the analysis of own results of the Danglobe Project (Elek & Lövei 2007, 2017), a hypothesis was formulated under the name "differential activity hypothesis", which suggests that the activity profiles of individual species reflect habitat quality. In an unfavourable habitat, we expect that the beetles have high activity in the early part of the season, because their fat reserves are depleted and their survival will depend on finding food immediately after emergence from hibernation. Most generalist predators that emerge from winter inactivity find themselves in this situation (Bilde et al. 2000). After an initial burst of activity, they are forced to emigrate from such an unfavourable habitat due to lack of food. Beetles in less favourable habitats can also show late bursts of activity density, when individuals developed in other, more favourable habitats may "spill over" into habitats with less favourable conditions (Rand et al. 2006). If only yearly totals are considered (as is the case for most published studies in the Globenet Project, e.g., Niemelä et al. 2002, Magura et al. 2004), these aspects remain hidden. The differential activity hypothesis compares individual species and can be applied to common species that occur in the habitats to be compared.

The aim of this study is to demonstrate the usefulness of the "p-p plot" technique in the comparative analysis of ground beetle activity. This technique was used to test the above-described "differential activity hypothesis" at different urbanisation stages.

Methods

Comparing seasonal activity among different urbanisation stages

Seasonal activity among the different urbanisation stages was compared using the percentile-percentile plots based on the following steps:

1. Prepare quantile plots (Fazekas et al. 1997) or tables of the two capture series to be compared.
2. Plot the two cumulative capture series against each other. Be aware that the points have to represent the cumulative captures at the same time in the two data series. Occasional interpolation of one data point is allowed. Let us assume that the first data point along the x -axis is 20%. To find the corresponding data point in series 2, first, find the date belonging to the point on the graph of series 1 (constructed as indicated under point 1), then look up the value on that same date on series

3. Do this for all points along the seasonal graph. If the two datasets have the same seasonal distribution, the points will fall on the diagonal line (Fig. 4.1.1). Deviations from this reference line indicate differences in seasonal activity (depicted, for demonstration only, by two other lines on Fig. 4.1.1).

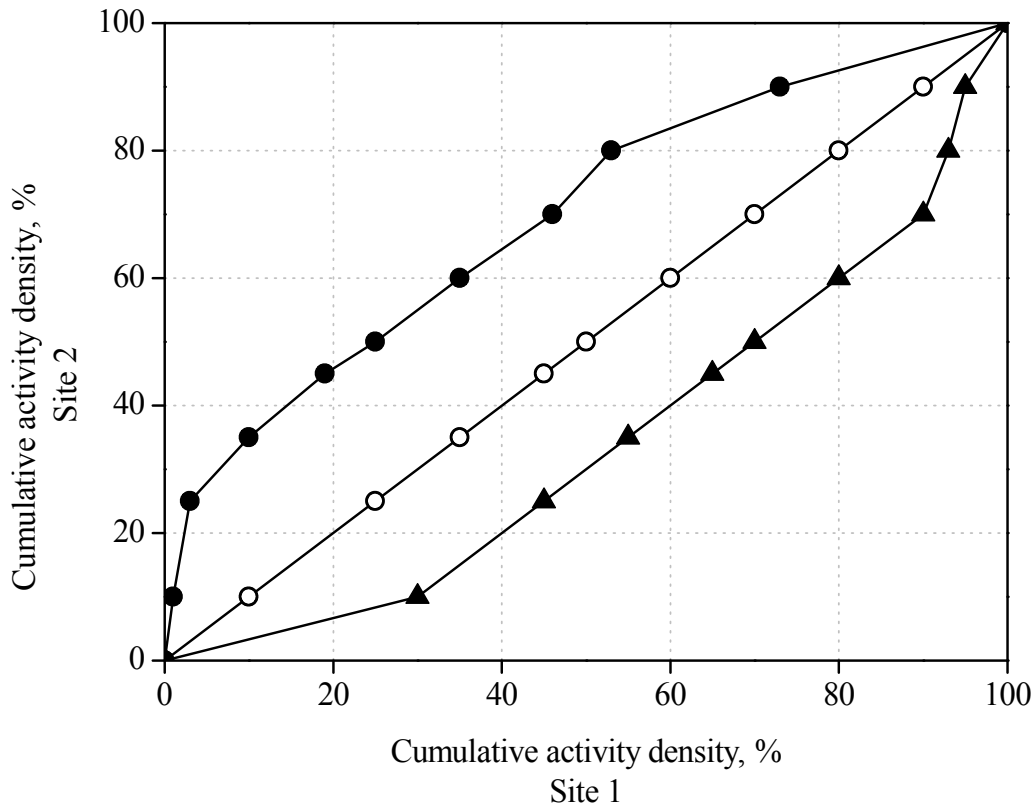


Figure 4.1.1 An example of the comparative activity plots of three hypothetical pairs of datasets. The one with empty circles indicates two activity curves that are not different from each other. The curve with full circles indicates a relationship where activity at Site 2 is consistently earlier than at Site 1, and the curve with triangles indicates that activity at Site 1 is earlier than at Site 2.

While the two data series do not have to be collected during precisely the same period, the time axis over which the seasonal graph is compared should be identical. In such cases, the start of the graph should be the date of the series with the earlier start, and the end should be that of the latter one. All comparisons should use identical time axes. To help interpretation, dates can be indicated as labels along the diagonal axis (see Figs 4.1.2-4).

We suggest that these plots are called “comparative activity plots”. In order to illustrate their use, the seasonal activity of some common ground beetle species was compared. Species with ≥ 10 individuals/year collected at each of the three studied habitats (rural forest, suburban and urban) in both years were used for further analyses. Three species fulfilled these conditions: *Pterostichus melanarius* Illiger 1798, *Nebria brevicollis* F. 1792 and *Carabus nemoralis* Müller 1764.

Results

Seasonal activity comparisons, Pterostichus melanarius

The activity density of this species was the highest in the urban park in both years (Table 4.1.1). The comparative graphs (Fig. 4.1.2) indicate that the seasonal activity was largely similar in the three habitats in 2004 (except for an early activity burst in the suburban habitat). In 2005, beetles in the rural forest were active earlier than in the suburban one or, to a lesser degree, in the urban park (Fig. 4.1.2). In the suburban-urban comparison, activity was similar in the early part of the season, but ended earlier in the suburban habitat than the urban one (Fig. 4.1.2).

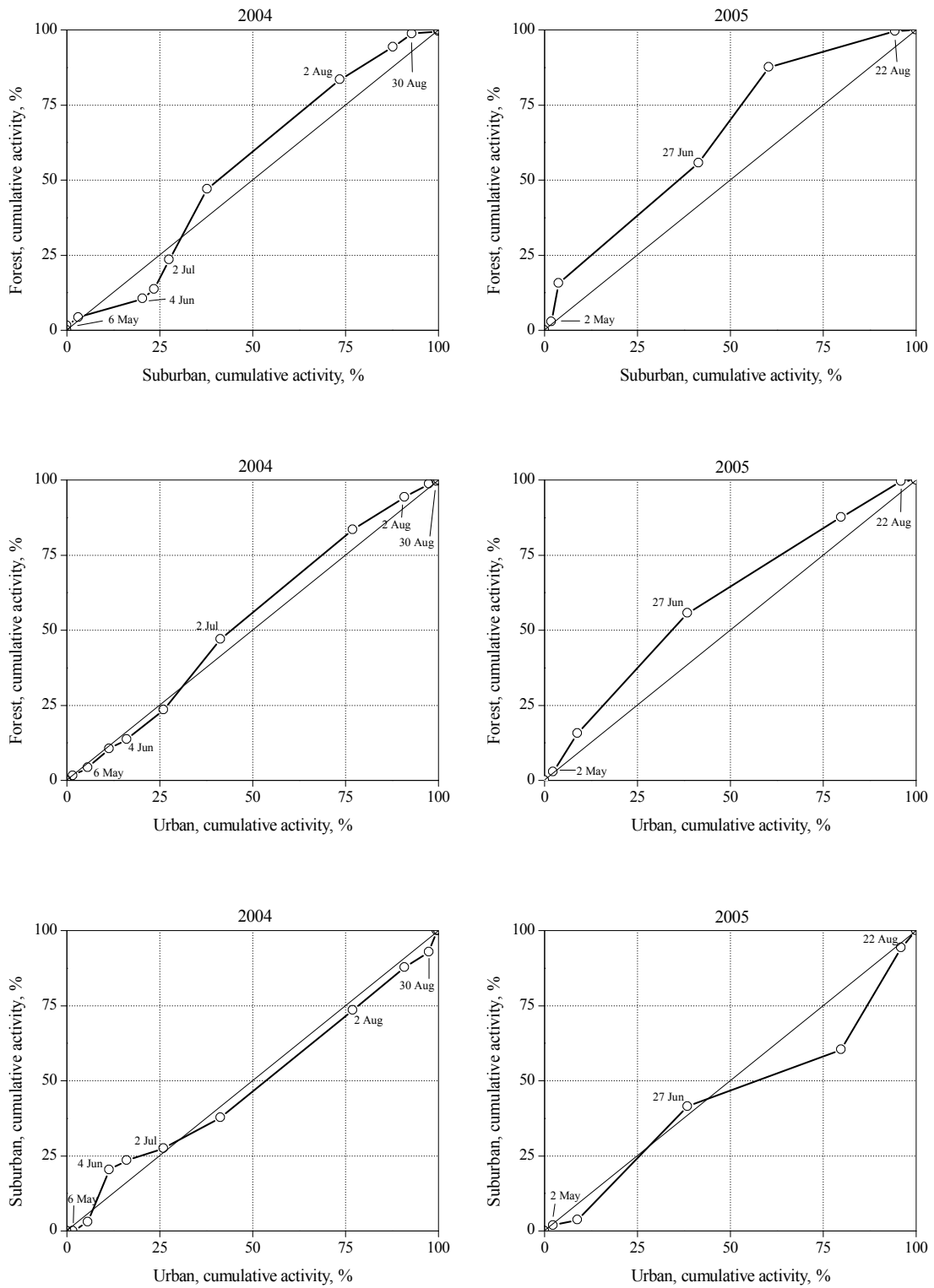


Figure 4.1.2 Comparative activity plots for *Pterostichus melanarius* in rural, suburban and urban habitats at Sorø, Denmark, during the sampling periods in 2004 and 2005.

Seasonal activity comparisons, Nebria brevicollis

The activity density of this species was highest in the urban park in both years (Table 4.1.1), but the species displayed large differences in seasonal activity among the different habitats (Fig. 4.1.3). Adults were active earlier in the rural forest and urban park than in the suburban forest in 2004 (Fig. 4.1.3). This difference was especially large between the urban park and suburban forests (Fig. 4.1.3). In 2005, the activity density of *N. brevicollis* was higher than in 2004 (Table 4.1.1), especially in the latter half of the season, regardless the fact that similar between-habitat trends were found.

Table 4.1.1 Activity density (no. of individuals/trap x week) of *P. melanarius*, *N. brevicollis* and *C. nemoralis* in forests or forest fragments, and their total numbers captured along an urbanisation gradient.

Year, habitat	Species		
	<i>Pterostichus melanarius</i>	<i>Nebria brevicollis</i>	<i>Carabus nemoralis</i>
2004			
Rural forest	629	173	148
Suburban	98	115	271
Urban	1780	846	309
2005			
Rural forest	275	259	46
Suburban	53	302	170
Urban	471	891	85
Total	3306	2586	1029

Seasonal activity comparisons, Carabus nemoralis

The activity density of this species was the highest in the urban park in 2004, while in the suburban forest in 2005 (Table 4.1.1). In 2004, the activity in the rural forest and suburban one was similar, apart from a late summer burst of adult activity in the rural forest (Fig. 4.1.4). This trend was much more pronounced in 2005 (Fig. 4.1.4). The rural forest-urban park comparison indicated that adults were active earlier in the urban than the rural habitat, and showed a steep autumn activity increase in the late season, especially in 2005 (Fig. 4.1.4). Comparing the suburban and urban habitats, both the spring and autumn activities started earlier in the urban than the suburban habitats in both years (Fig. 4.1.4).

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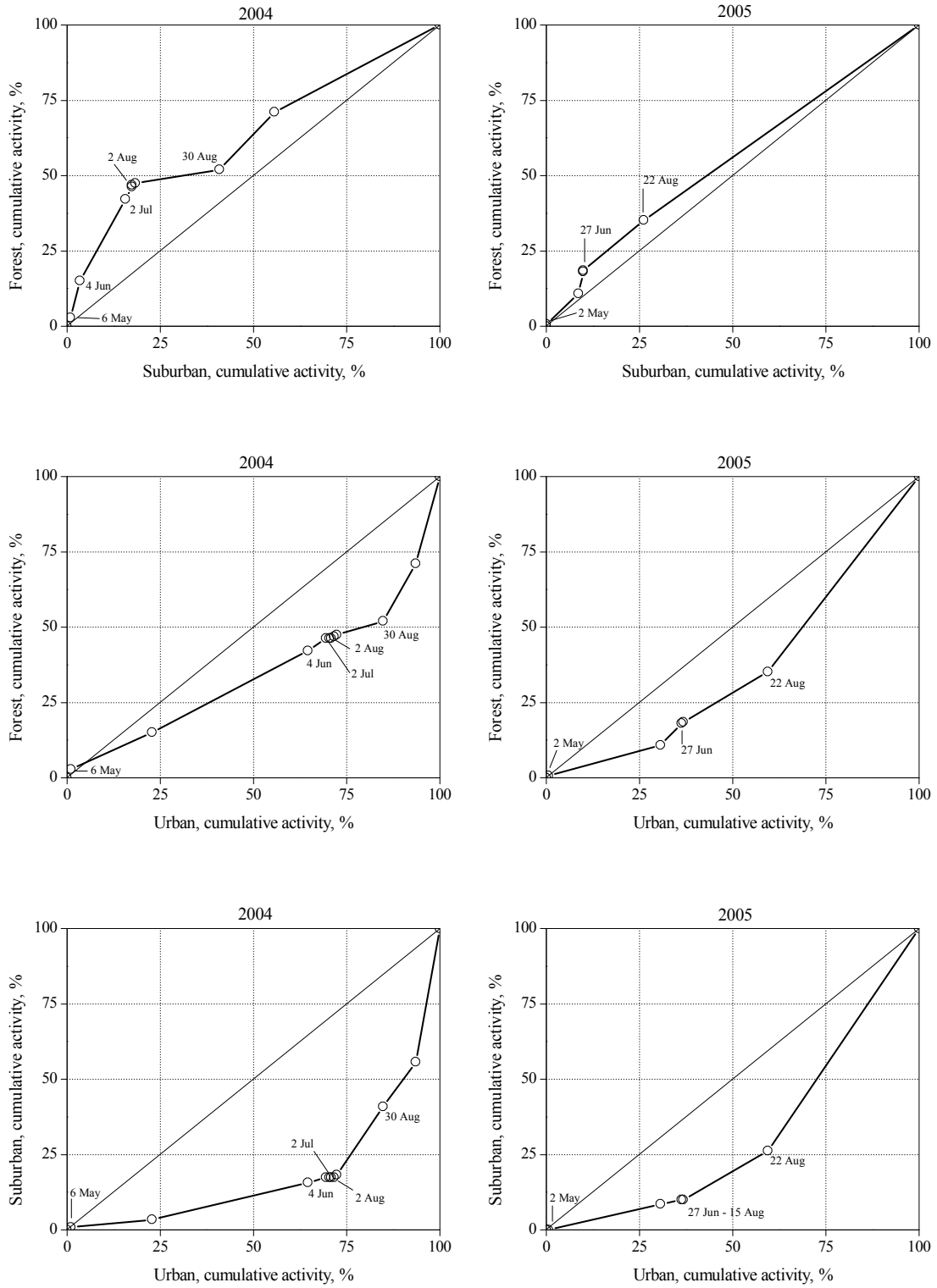


Figure 4.1.3 Comparative activity plots for *Nebria brevicollis* in rural, suburban and urban habitats at Sorø, Denmark, during the sampling periods in 2004 and 2005.

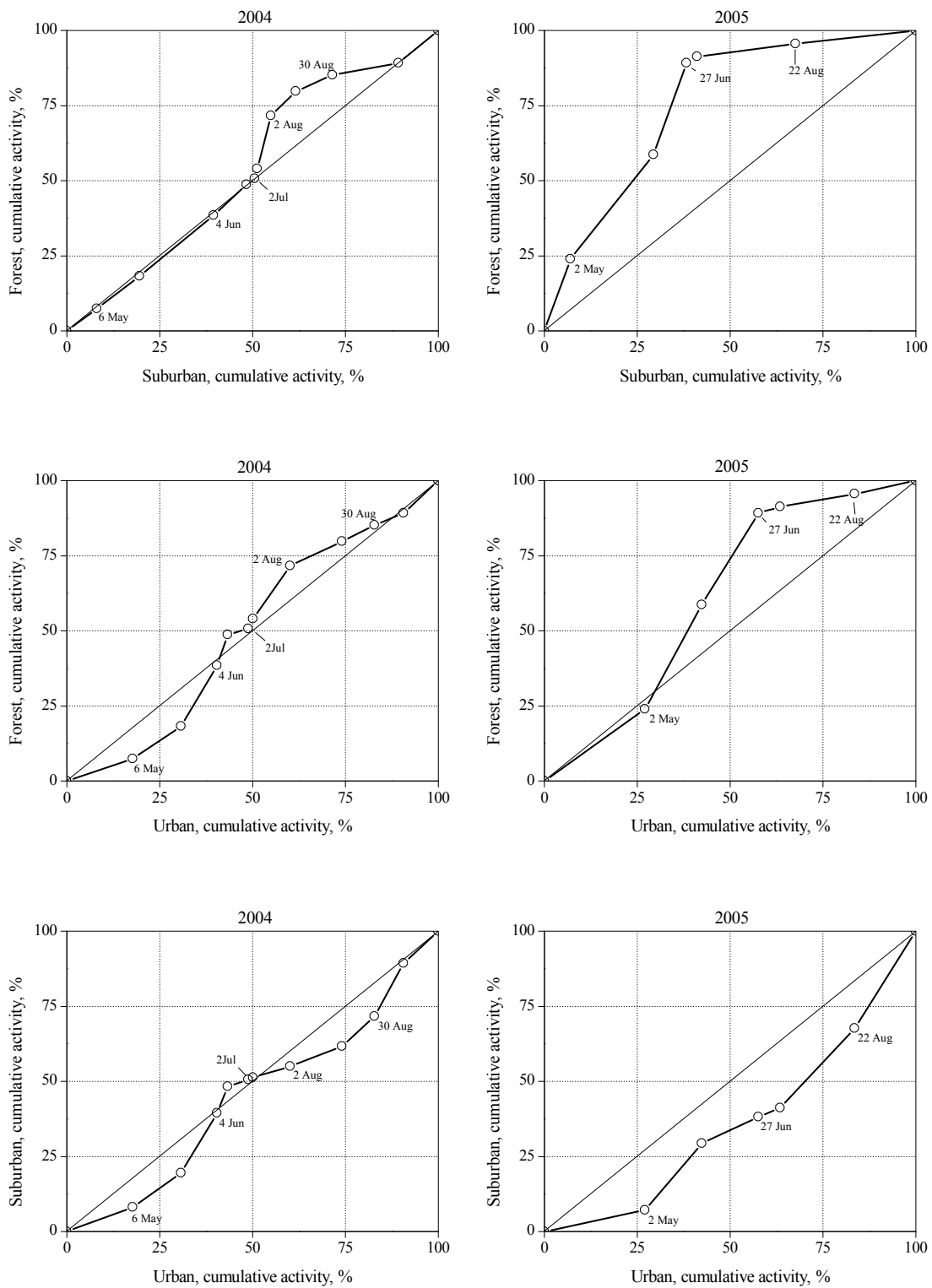


Figure 4.1.4. Comparative activity plots for *Carabus nemoralis* in rural, suburban and urban habitats at Sorø, Denmark, during the sampling periods in 2004 and 2005.

Discussion

Carabids in the temperate region are generally most active during spring and summer, and show clear seasonality (Thiele 1977). This was also the case in Sorø, Denmark, but a remarkable difference was found in the activity pattern of the common ground beetle species in the habitats that belong to different urbanisation stages.

P. melanarius, a habitat generalist (Thiele 1977, Desender et al. 2008) was less affected by urbanisation, showing no major differences in seasonal activity among the habitats and years. This species hibernates as an adult, which can enable it to survive (and reproduce) in suboptimal habitats (Lövei et al. 2018).

N. brevicollis is a more strictly carnivorous species, and its activity pattern showed noticeable differences among the habitats and dates. This species was more active in the urban park than elsewhere, mainly in the early summer period. During this time changes in the abundance occurred rapidly, because of the emergence of teneral adults which led to an explosion in the number of individuals (Penney 1969). The comparison also revealed that the suburban forests were not optimal for this species: large numbers only occurred here after the appearance of the new generation, manifested in an activity burst in the urban habitat. The beetles captured later in the suburban forests could be immigrants from the urban park. In the rural forest, the delayed activity peak could indicate a slower development of larvae, which could reflect the lower temperatures occurring in such habitats (Magura et al. 2008, Lövei et al. 2018).

C. nemoralis is a habitat generalist (Thiele 1977, Desender et al. 2008). Differences between years, more in numbers than in the shape of the comparative curves, could be influenced by the overwintering success of the adults, indicating the suitability of their overwintering habitats. In this respect, the value of suburban forests and urban park was similar, while the rural forest seemed to be better.

In several cases, an earlier onset or higher level of activity was found in the urbanised area than in the other habitats. As forest fragments were smaller in the urbanised habitats than in the two other urbanisation stages, the "heat island" effect of urban areas (McKinney 2006) can make the temperature in these fragments higher, extending the activity period of adults and allowing faster development of larvae.

Studying the seasonal dynamics of invertebrates is important, because it can help to clarify the ecological pattern against a background of confounding factors (Ewers & Didham 2006).

Differential changes in activity curves hinted at differences in habitat suitability for larval

development (in *N. brevicollis*) or overwintering (in *C. nemoralis*), generating hypotheses about the causes of these differences that can be tested in experiments. Other factors, such as the density, kind and activity of natural enemies (Lövei & Sunderland 1996), prey availability, and habitat structure (Thiele 1977) could also influence activity, directly or indirectly.

Using comparative activity (p-p) plots revealed patterns not evident when comparing sites with traditional seasonal-activity curves. Comparative p-p plots can be useful for a more sophisticated analysis of invertebrate reactions to changes in habitat conditions. Quantification of differences for comparisons would be possible by quantifying the area of deviation from the diagonal line, similar to the suggestions to evaluate differences in size distribution by Magura et al. (2006). Like many graphical methods, comparative p-p plots can be a very useful tool to conceptualise complicated phenomena to generate hypotheses and to direct further analyses (Cleveland 1993).

4.2 Recording fine-scale movement of ground beetles by two methods: potentials and methodological pitfalls

Tracking periods of small animals, especially ground-dwelling insects, are limited only to a period of a few days or weeks due to the limited battery life of VHF transmitters. To maximize the cost/benefit ratio in obtaining a sufficient amount of high-resolution movement data, ground-dwelling insects are tracked as often as possible, usually every few hours. Covered distances per one step barely exceed a few tens of meters and these studies focus on daily movement patterns within and between small habitat patches (e.g., Riecken & Raths 1996, Negro et al. 2017, Růžicková & Veselý 2018). Nevertheless, the estimated positions of commercially available GPS devices (to record exact coordinates) are relatively accurate above 3 m distance, but below that distance the measurement error progressively increases (Ranacher et al. 2016). As this is the range usually covered daily by walking insects, the measurement error can add a bias when a trajectory is recorded by a GPS device, hitherto this issue is routinely ignored in movement ecology studies for insects (but see Fernández et al. 2016).

Although several methods are available for recording animal paths without remote-sensing techniques, their utilization requires experience for the correct estimation of parameters of each movement step (Turchin et al. 1991, Fisher et al. 2020b). The “coordinate geometry” method, also called the distance-bearing method, can be an ideal option to avoid the bias of the GPS method at fine-scale mapping (Turchin et al. 1991). In distance-bearing (DB), the coordinates of the target location are obtained from the last known position by using the directly measured distance and the compass azimuth (bearing; Baars 1979, Wallin & Ekblom 1988, Robinson et al. 2020). This method has a long tradition for recording paths of insects at fine spatio-temporal scales; nevertheless, it has widely been used only in studies of butterflies as they can be relatively easily followed due to their conspicuous flying behaviour (e.g., Schultz & Crone 2001, Skórka et al. 2013, Fisher et al. 2020a). In studies on movement ecology of other insect groups, including ground-dwelling beetles, distance-bearing has largely been abandoned due to the rapid development of easy-to-use handheld GPS devices (but see Růžicková & Veselý 2018).

Albeit fine-scale movement maps generated by using either distance-bearing or GPS can differ, no quantification of such difference exists so far. Inaccurate positional data might completely mask a biological signal extracted from the movement path, such as microhabitat resource use (Bradshaw et al. 2007). Habitats are not homogeneous, but consist of a spatial mosaic of different microhabitat patches. For instance, the distribution of rocks, bare soil, dead woody debris, leaf litter, or shrubs

changes within a few meters in the managed temperate forest (Negro et al. 2014, Elek et al. 2018). These patches can have different functions, serving as shelters, overwintering, oviposition, or foraging sites and ground-dwelling species show a non-random distribution associated with a certain microhabitat (Niemelä et al. 1992a, Pearce et al. 2003, Wehnert & Wagner 2019). Thus, it is important to be able to precisely describe microhabitat selection on fine spatial scales based on individual movement for understanding how a particular species persists in its environment and consequently adjust possible management (Negro et al. 2014).

In this chapter GPS and distance-bearing approaches will be assessed in recording fine-scale movement in two experiments where we considered simulated and real trajectories made by ground-dwelling insects. Carabid beetles were selected as one of the most frequently radio-tracked insect groups. In the first experiment, artificially generated trajectories were used based on movement parameters derived from already existing movement data for large species of the genus *Carabus*. As their step length between relocations rarely exceeds 20 meters within a few hours (e.g., Růžicková & Veselý 2018), it has been assumed that the measurement error up to this distance recorded by distance-bearing is lower than that of a GPS device. Therefore, we considered locations (hereafter fixes) obtained by distance-bearing as control and those recorded by the GPS method as biased ones, i.e., the measurement error represents the error of a GPS device. In the second experiment, we employed radio telemetry and tracked living specimens of *C. coriaceus* equipped by small VHF transmitters in an oak hornbeam forest. We recorded their fixes every four hours by both methods and hypothesized that additional factors interfering with GPS-signal, such as dense forest canopy and weather, could increase the measurement error and notably affect recorded movement parameters and trajectory profiles.

In particular, two major research questions were raised: (1) Is there any significant difference in the magnitude of measurement error between DB-measured and GPS-measured trajectories regarding distances and bearings? (2) If so, how can the measurement error bias a trajectory shape and consequent biological signal represented by the two distinct movement patterns stages for carabid beetles, the random walk and the directed movement, based on state-switching model estimates?

Methods

The first experiment was based on simulated fine-scale trajectories. Each generated trajectory was represented as a sequence of discrete consecutive fixes where each fix was defined by two parameters: step length (distance) and turning angle (bearing) between successive movements

(Kareiva & Shigesada 1983, Marsh & Jones 1988, Calenge et al. 2009). These parameters were generated in R 3.6.1 (R Core Team, 2020) for each fix separately in the following way:

(1) The step length in meters was selected in a four-step randomization process. First, 100 random numbers between 0.5 and 20.0 were generated using the “runif” function rounded to one decimal number. Minimal and maximal values corresponded with distances (in meters) usually covered by large *Carabus* species per one fix (existing data for *C. coriaceus*: Riecken & Raths 1996; *C. hungaricus*: Bérces & Růžicková 2019; *C. olympiae*: Negro et al. 2008, 2017; *C. ullrichii*: Růžicková & Veselý 2016, 2018). From this random set, we sampled 50 values using the sample function without replacement, and then five values were selected by the same function. As the final step, one value out of five was randomly selected for the step length to avoid the consistent error added by randomization by computers.

(2) The turning angle, an absolute turning angle towards a fixed point, i.e., magnetic north was selected in the same process as in the step length. As a primary random set, 100 integers between 1 and 12 were generated using the runif function following a uniform distribution. Here, 1 corresponded with 30° compass azimuth and 12 with 360/0° azimuth (i.e. towards north), thus having 12 discrete units per 30°. This randomization procedure helps to avoid any autocorrelation in turning angles, which can distort further simulations (Dray et al. 2010). The whole selection process was repeated until three trajectories were generated with 10 fixes and three trajectories with 20 fixes. As was already demonstrated by Turchin et al. (1991), this number of fixes per trajectory was sufficient to get an adequate description of individual movement.

The experimental site was a grassland with a few solitary trees to avoid possible additional GPS measurement errors due to dense vegetation and slope (Frair et al. 2010). The site was situated on the outskirts of Budapest, Hungary, on the western bank of the river Danube (47.4724°N, 19.0609°E). Approximately in the middle of the experimental area, we randomly chose a point of reference and its geolocation was recorded by a hand-held GPS device (Garmin Dakota 20, in WGS84 coordinate reference system, accuracy ~3 m). From this point, we manually built the trajectory (with predefined fixes generated above) using a measuring tape (0.3 cm accuracy) and a magnetic compass (1° accuracy) with a protractor. The GPS coordinates for each fix were recorded by the above-mentioned device. Only a single GPS logger was used. Thus, distance-bearing was used to build a particular trajectory and then its fixes were GPS-measured. The relationship between DB-measured and GPS-measured trajectories and measurement errors is described in Fig. 4.2.1. Magnetic declination was considered as an angular difference between the magnetic north (the direction of the compass needle) and the true geographic north. Its estimated value for the experimental site was +5.133°, i.e., towards the east (World Magnetic Model 2020). Each of the six

trajectories was built three times *de novo* from the same starting point with at least a one-day break between builds. All GPS coordinates were sampled only during sunny days with max. 20% cloud coverage to avoid any additional atmospheric interference. To sum up, 384 fixes in 24 trajectories were collected; six DB-measured and 18 (three repeats of six) GPS-measured tracks. Data sampling was conducted between April and June 2020.

In the second experiment, the radio-telemetry dataset of *C. coriaceus* was used as reported in chapter 3.2.

Data analyses

The same statistical approach was used in both experiments. To compare DB-measured and GPS-measured fixes, first, we had to obtain step lengths and bearings from GPS-measured coordinates. We used the “as.ltraj” function from the *AdehabitatLT* package which can compute several descriptive parameters of the trajectory from a set of GPS coordinates (see Calenge 2006 and Calenge et al. 2009 for details). In the created ltraj object, we considered two parameters: distance (dist) between successive fixes and absolute angle (abs.angle) between x-direction (longitude in this case) and the step direction (see Marsh & Jones 1988 for details). The latter parameter is originally provided in radians and with a different orientation than in the DB approach, so we converted it to compass azimuths where absolute angle 0 rad corresponded to 90° azimuth (east), $+\pi/2$ rad to 0° (north), $-\pi/2$ rad to 180° (south), and finally π rad to 270° (west, Marsh & Jones, 1988). Second, we obtained long/lat coordinates from DB-measured fixes using Azimuth and Distance Plugin (de Paulo et al. 2016) in QGIS 3.4.2 (Version “Madeira”, QGIS Development Team 2019). The plugin can draw a trajectory from a list of distances and compass azimuths. As a starting point, we used GPS coordinates of the reference point (in the first experiment) or beetles’ releasing point (in the radio-tracking experiment) to concatenate the DB-measured trajectory in long/lat coordinate system and to ensure that the corresponding pair of trajectories (DB-measured and GPS-measured) starts from the same point. When the trajectory was drawn, we extracted its long/lat coordinates. The correlation between DB- and GPS-measured long/lat coordinates was quantified by Pearson correlation. We calculated differences (measurement errors) between DB- and GPS-measured distances and bearings for the corresponding pair of fixes (Fig. 4.2.1). If no measurement error existed, the difference was zero. For distance error, the positive values indicated larger GPS-measured distances than DB-measured ones and vice versa if negative. In the case of bearings, absolute values were used due to the circular nature of the variable. To test the relation of both types of errors to DB-measured distances and bearings and whether these errors can be affected by fix

order, we used linear mixed models with a normal distribution and identity link function (the “lmer” function from the *lme4* package, Bates et al. 2013). In a single-argument model, DB-measured distances, bearings, the fix order in the trajectory were considered as a fixed effect and the track ID as a random effect. We also tested whether the total length of the trajectory (i.e., the sum of all steps lengths) differs between recording methods. The explanatory power of each model was tested by marginal R^2 for fixed effects and conditional R^2 for random effects using the “r.squaredGLMM” function from the *MuMIn* package (Bartoń 2021). In the radio-tracking experiment, carabid beetles often exhibited no activity between consecutive fixes (sensu Riecken & Raths 2016, Růžicková & Veselý 2018 for other species). These passive fixes were excluded from linear mixed models as measurement errors in distances and bearings could be calculated only from active fixes.

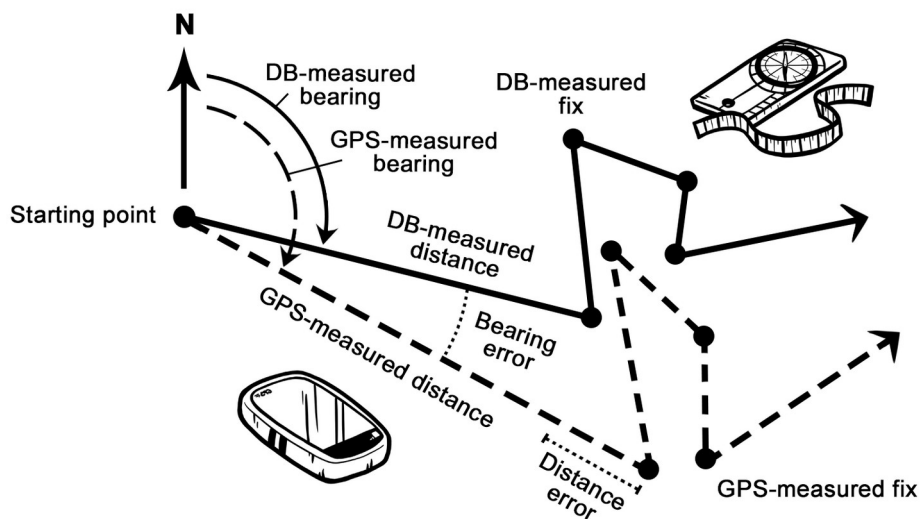


Figure 4.2.1 Overview of two methods, distance-bearing (DB) and GPS, and their expected differences in recording fixes. DB-measured trajectory (solid line) was recorded by magnetic compass with a protractor and measuring tape, while fixes of GPS-measured trajectory (dashed line) were recorded by GPS device. Due to measurement errors in distances and bearings (dotted line) of the employed GPS device, GPS-measured trajectory differs from DB-measured one. For a better visibility, the movement parameters including error terms are shown only between the first two fixes but in fact, they were measured for every fix.

For segmenting both DB- and GPS-measured trajectories into distinct movement states, the hidden Markov models were used (HMMs; Michelot et al. 2016). In carabids, two distinct movement stages can be distinguished. A random walk is described by short step length and high variation in bearings; this is characteristic for the foraging behaviour and the presence of suitable habitat (Baars 1979). Long step distances with the same turning angles are characteristic of a directed movement that usually results as an indented migration from one habitat to another (Baars 1979, Kareiva & Shigesada 1983). For a two-state trajectory segmenting, first, the HMM was fitted only on the DB-

measured trajectories using the “fitHMM” function from the *moveHMM* package (Michelot et al. 2016) to ensure the optimal decoding of the random walk and the directed movement. As initial values of the model parameters, the mean step length was set at 1 m for the random walk and 10 m for the directed movement, respectively. Since the gamma distribution was used to model step length, we set the initial SD of the same order as the mean value of a particular movement state. The mean turning angle was π for the random walk with an angle concentration of 0.5. The concentration parameter close to zero corresponds with a uniform distribution of turning angles (i.e., undirected movement); the higher it gets, the more directed movement is. For the directed movement, the mean turning angle was set at 0 rad with a concentration of 2.5 (see Michelot et al. 2016). For the radio-tracking experiment, zero inflation was specified as 0.5 for both movement states. Subsequently, the model with the same parametrization was fitted to GPS-measured trajectories. Under the fitted HMM, each trajectory was decoded by the Viterbi algorithm into the sequence of two movement states and plotted as a trajectory map, where each fix was coloured according to a particular movement state. We counted the number of random walks and directed movements for each trajectory. Generalized linear mixed effects model (the “glmer” function) with a binomial distribution and logit link function was used to test whether movement states (represented as a proportion of random walk) differed between DB-measured and GPS-measured trajectories. The response was coded as a two-column matrix of (random walk, directed movement) using the `cbind` function (Grueber et al. 2011). In the model, the recording method (DB vs. GPS) was a fixed effect and a track ID was a random effect.

Results

Artificial trajectories

In total, we collected 384 fixes, including starting points, for 24 trajectories; six DB-measured and 18 (three repeats of six) GPS-measured tracks. The comparison of DB-measured and GPS-measured long/lat coordinates showed a strong correlation in the longitude (Pearson $r = 0.981$, $t = 84.815$, $df = 267$, $p < 0.001$, Fig. 4.2.2a) but less in the latitude (Pearson $r = 0.929$, $t = 41.007$, $df = 267$, $p < 0.001$, Fig. 4.2.2b) suggesting greater measurement error in latitudinal coordinates.

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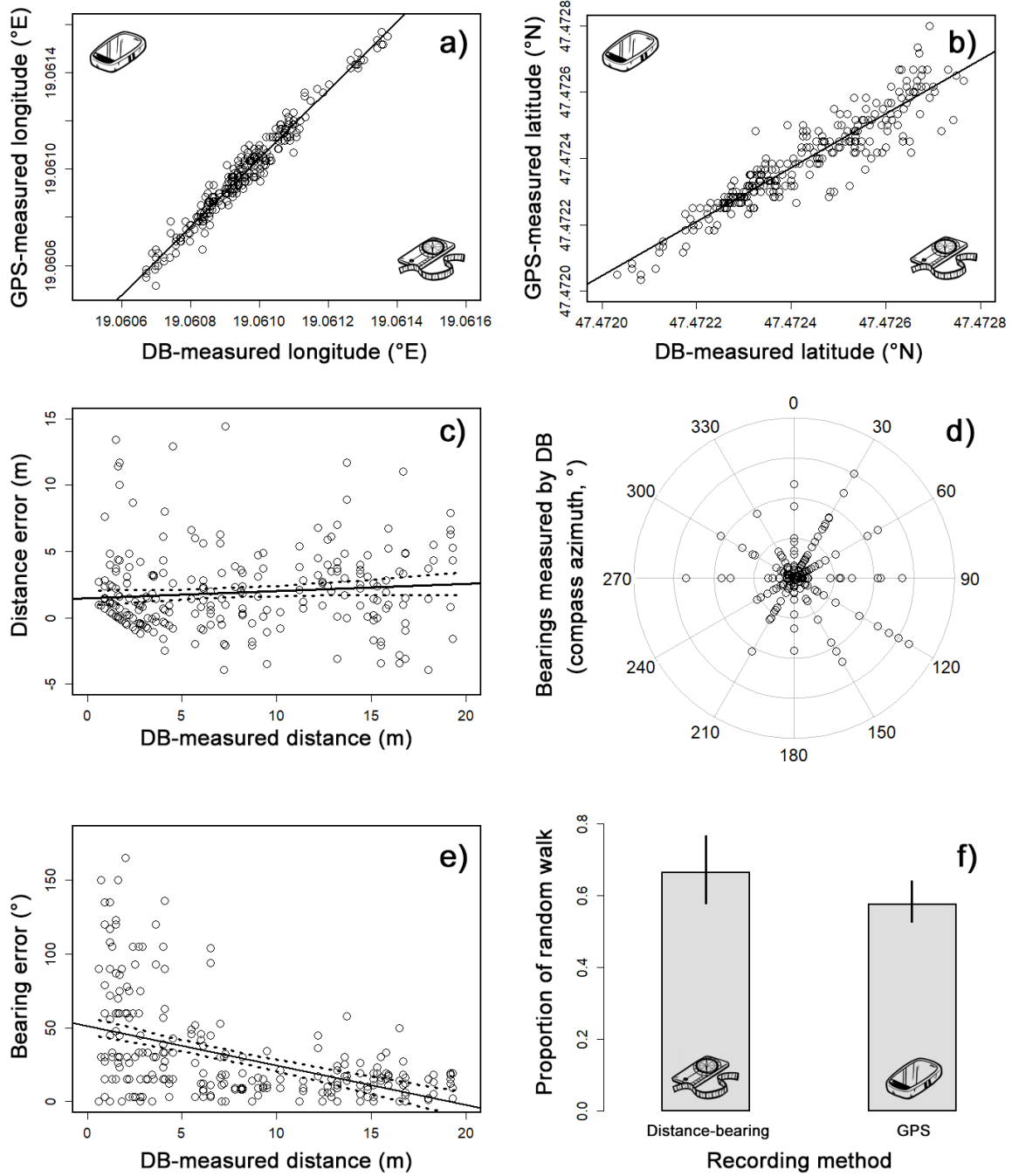


Figure 4.2.2 The correlation between DB-measured and GPS-measured longitude (a) and latitude (b) coordinates from the experiment with artificial trajectories. The relationship between DB-measures distances (c), bearings (d) and their errors; and between bearing errors and DB-measured distances (e). The concentric circles in (d) represent the magnitude of bearing errors. The proportion of random walk as one of the movement states in a particular recording method is shown on (f). Dashed lines and whiskers represent a 95% confidence interval.

Table 4.2.1 Comparison of fine-scale trajectories recorded by two methods: distance-bearing and GPS from the experiment with artificial trajectories (A) and radio-tracking of six *Carabus coriaceus* individuals (B). Total length of the trajectory is a sum of all step lengths in a particular trajectory. Step length represents the mean (minimum; maximum) distance covered in one movement step. The number of fixes in radio-tracking experiment shows only active fixes with recorded movement activity of tagged beetles. Trajectory IDs follow the same numbering as in Fig. 4.2.1 and Fig. 4.2.4.

	ID	No. of fixes	Distance-bearing		GPS	
			Total length (m)	Step length (m)	Total length (m)	Step length (m)
A)	1	10	85.0	8.5 (1.2; 18.3)	104.3	10.4 (1.6; 23.8)
	2	10	88.1	8.8 (1.5; 19.2)	117.7	11.9 (2.4; 25.8)
	3	10	66.3	6.6 (0.9; 15.1)	78.3	7.9 (1.6; 18.4)
	4	20	150.0	7.5 (0.7; 19.3)	184.9	9.3 (1.6; 27.7)
	5	20	134.6	6.7 (0.6; 16.8)	153.8	7.7 (1.6; 21.7)
	6	20	144.1	7.2 (0.9; 19.2)	193.9	9.7 (1.6; 25.4)
B)	1	11	65.4	5.9 (0.5; 14.7)	105.3	9.6 (2.2; 24.0)
	2	4	25.4	6.4 (0.5; 19.8)	35.9	9.0 (2.4; 21.4)
	3	4	8.0	2.0 (0.5; 4.7)	22.9	5.7 (3.7; 9.4)
	4	4	33.9	8.5 (1.2; 23.1)	89.2	22.3 (1.5; 48.1)
	5	3	3.9	1.3 (0.5; 1.8)	14.6	4.9 (2.4; 6.9)
	6	6	43.3	7.2 (1; 21.3)	40.0	6.7 (1.9; 18.16)

Distances recorded by GPS device were on average 1.878 m (SEM = 0.181 m) larger than the DB-measured ones and the size of the measurement error did not change with increasing covered distance (Fig. 4.2.2c). For the total length of the trajectory, the trajectories recorded by GPS were significantly longer than the distance-bearing ones by about 28.1 m (Tables 4.2.1 and 4.2.2). The average bearing error of GPS was 31.330° (SEM = 2.066°) and it was evenly distributed among all directions (Fig. 4.2.2d). However, the size of the bearings error was significantly higher at shorter than longer distances (Table 4.2.2, Fig. 4.2.2e). The number of fixes recorded in a trajectory did not have an effect either on distance error or on bearing error.

HMMs revealed that the proportion of random walks in DB-measured trajectories was 8.89% higher than in those recorded by GPS device but this effect was not significant (Table 4.2.1, Fig. 4.2.2f); in other words, slightly more steps were described as directed movement in GPS-measured trajectories. The transition probability between movement states was 48.35% from random walk to directed movement and 69.48% in the opposite direction.

Table 4.2.2 The results of performed models from the experiment with artificial trajectories, the significant effects are in bold. The response variables 'distance error' and 'bearing error' were based on the differences between GPS-measured and DB-measured movement parameters. The explanatory power of the models was tested by marginal R^2 for fixed effects only and conditional R^2 for random effects (here as a track ID).

Models	χ^2	df	p	marginal R^2	conditional R^2
Distance error ~ DB-measured distance	2.702	1	0.100	0.009	0.085
Bearing error ~ DB-measured bearing	14.254	11	0.219	0.049	0.075
Bearing error ~ DB-measured distance	74.684	1	< 0.001	0.211	0.245
Distance error ~ fix order	0.218	1	0.641	0.001	0.079
Bearing error ~ fix order	1.469	1	0.226	0.005	0.022
Total trajectory length ~ recording method	16.946	1	< 0.001	0.070	0.905
Proportion of random walk ~ recording method	2.413	1	0.120	0.009	0.009

Radio tracking of *Carabus coriaceus*

Radio-tracking of six *Carabus coriaceus* individuals (Fig 4.2.4a) in the forest gave us, in total, 320 fixes, including releasing points, i.e., 160 for a particular recording method. Due to behavioural constraints of the species, only 64 fixes (32 per method) were with activity (Table 4.2.1). We found a strong correlation between DB- and GPS-measured longitude (Pearson $r = 0.987$, $t = 33.230$, $df = 30$, $p < 0.001$, Fig. 4.2.3a) as well as latitude (Pearson $r = 0.985$, $t = 31.809$, $df = 30$, $p < 0.001$, Fig. 4.2.3b). Distances recorded by GPS were on average 3.992 m (SEM = 1.718 m) larger than those recorded by distance-bearing and distance error significantly decreased with increasing covered distance (Table 4.2.3, Fig. 4.2.3c). The mean bearing error was 71.639° (SEM = 10.281°) and it was evenly distributed in all directions (Fig. 4.2.3d). Bearing error slightly decreased towards larger distances but this trend was not significant (Table 4.2.3, Fig. 4.2.3e). The total length of trajectory was on average 21.3 m longer when recorded by GPS than distance-bearing (Table 4.2.1 and 4.2.3). Concerning movement patterns, the proportion of the random walk was slightly but not significantly higher when trajectory was recorded by distance-bearing than GPS (Table 4.2.3, Fig. 4.2.3f). However, the measurement error, especially at short distances, notably disturbed trajectory profiles resulting in completely different profiles (Fig. 4.2.4b and 4.2.4c).

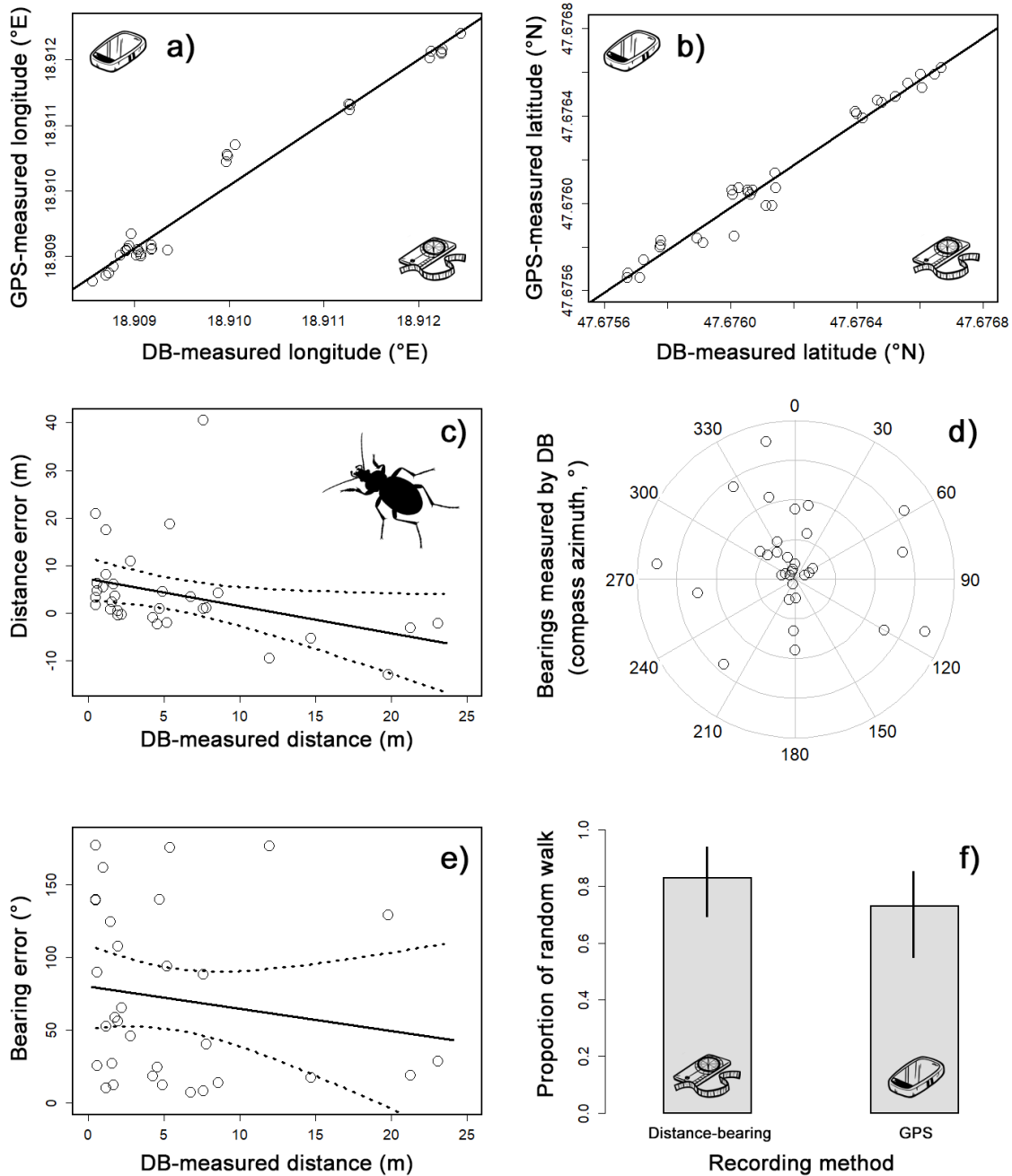


Figure 4.2.3 An experiment with fine-scale radio tracking of *Carabus coriaceus* in a temperate forest illustrating the impact of the measurement error on movement parameters recorded by GPS device. The comparison of DB-measured and GPS-measured longitude (a) and latitude (b) coordinates showed their strong correlation. The relationship between DB-measured distances (c), bearings (d) and their errors are displayed as well as between bearing error and DB-measured distances (e). In (d), the concentric circles represent the magnitude of bearing error. The proportion of the random walk as one of the movement states is shown on (f). Dashed lines and whiskers represent a 95% confidence interval.

Table 4.2.3 The results of performed models from the radio-tracking experiment, the significant effects are in bold. The response variables 'distance error' and 'bearing error' were based on the differences between GPS-measured and DB-measured movement parameters. The explanatory power of the models was tested by marginal R^2 for fixed effects only and conditional R^2 for random effects (here as a track ID).

Models	χ^2	df	p	marginal R^2	conditional R^2
Distance error ~ DB-measured distance	5.833	1	0.016	0.146	0.263
Bearing error ~ DB-measured distance	0.815	1	0.366	0.025	0.041
Total trajectory length ~ recording method	5.744	1	0.017	0.116	0.779
Proportion of random walk ~ recording method	1.551	1	0.213	0.044	0.219

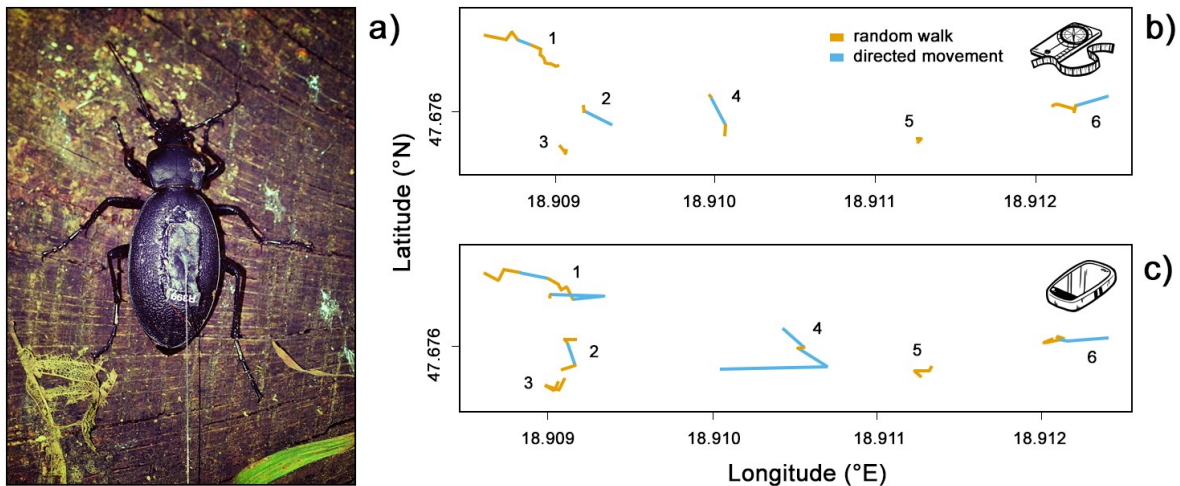


Figure 4.2.4 Female of *Carabus coriaceus* with an attached radio transmitter (a). Trajectories (1-6) decoded by the Viterbi algorithm into two movement states noticeably differed in their shapes between DB (b) and GPS (c) recording methods.

Discussion

Obtaining precise positional data is challenging, especially in fine-scale movements of walking insects such as carabids. Here we showed that fixes recorded by a GPS device considerably differed from those measured by distance-bearing due to errors in both distances and bearings leading to different trajectory shapes. Moreover, this measurement error was higher in the radio-tracking experiment due to other confounding factors such as dense canopy cover and rainy weather. Rather than using a high-precision professional GPS logger, we collected all geo-coordinates by a commercially available device. These units are commonly utilized by researchers in the field and likely have a similar magnitude of measurement error (e.g., Fernández et al. 2016, Ranacher et al. 2016, Růžicková & Veselý 2016). Therefore, our findings may help the design, especially the methodological aspects of future studies focused on movement in different habitats at a fine spatio-temporal scale. We highlight that the distance-bearing method for recording fixes may overcome the

problem with the measurement error of GPS devices, especially at short distances in the order of a few meters.

The magnitude of measurement error

In the experiment with artificial trajectories, the measurement error for the distance was nearly 2 m and did not increase with the greater distance covered. This contradicts the results of Ranacher et al. (2016) who found that overestimation of GPS-measured distances tended to rise with increasing distances due to low spatial autocorrelation of distant locations. Previously, only Fernández et al. (2016) tested the reliability of recorded positions in the fine-scale movement of butterflies and reported the mean distance error as 0.033 m, with a maximum value of 0.25 m for a similar, hand-held GPS device. Their values were a magnitude lower than in this study, probably because of the different methods of quantification. The authors used coordinates of easily recognizable landmarks, such as solitary trees or shrubs, for calibrating butterfly positions. Benchmarking is based on an already known fixed location and usually produces a measurement error below 1 m (Robinson et al. 2020). Contrarily, geo-coordinates obtained from moving large animals without any reference position may suffer from relatively high measurement error which, in some cases, can exceed 100 m (Frair et al. 2010, Montgomery et al. 2010). Although these studies were published a decade ago and technological advances made the precision of GPS devices better since then, the current measurement error still remains at ≤ 3 m (Ranacher et al. 2016). It seems to be possible to overlook errors in the distance in flying, mobile species with high dispersal power (e.g., butterflies, dragonflies, flying beetles) where the one movement step exceeds one hundred meters (Rink & Sinsch 2007), but not in ground-dwelling insects that cover much less distance on the ground. Several *Carabus* species cover only a few meters between two tracking sessions at the temporal scale in a couple of hours (Riecken & Raths 1996, Negro et al. 2017, Růžicková & Veselý 2018). As the distance recorded by GPS device is higher due to measurement error, it leads to overestimation of the total distance in movement paths. This can be an issue if GPS-measured distances are used for dispersal estimations. The overestimated dispersal capacity of target species may lead to ineffective management practices (e.g., forming corridors or stepping stones in fragmented landscapes), reducing species' ability to disperse between suitable (micro)habitat patches as the distance between them is too large to cover. Hitherto, if the tagged individual did not move between two tracking sessions as ground beetles frequently do (see Riecken & Raths 1996, Bérces & Růžicková 2019), but the geo-coordinates are recorded for both events, the measurement error may indicate false movements.

The bearing error was approximately 31° from the estimated directions. However, it was significantly higher at short distances, resulting in completely different shapes of trajectories. For GPS collars, Jerde & Visscher (2005) reported the same issue at the large spatial scale where bearings were accurate only when the observed distance between two fixes was large in relation to the measurement error of a GPS device. They suggested re-scaling the temporal resolution of sampling to increase the distance covered by tracked individuals between consequent measurements, for example by obtaining a fix only every 2 h instead of every 5 min (Jerde & Visscher 2005). The proposed solution is, however, not suitable for ground-dwelling beetles due to the fine temporal scale. Usually, they are tracked every few hours to obtain a high resolution of movement data. It can take several days until the tracked individual walks far enough to overcome the measurement error of the employed GPS device. Moreover, further reduction of sampling resolution is not possible due to the short battery life of used VHF transmitters which is a couple of weeks at maximum.

The possible bias of the biological signal and additional interfering factors

Shapes of GPS-measured trajectories differed substantially from those recorded by distance-bearing in both experiments. Hidden Markov Models showed a slight underestimation of random walks in the GPS-measured trajectories. The measurement error can increase in rainy weather as well as in other habitat types, especially in densely overgrown vegetation, where the closed (and occasionally wet) canopy acts as a strong interfering factor for GPS signals (Frair et al. 2010). A higher measurement error may bias a trajectory profile and consequently, state-space modelling may result in a higher proportion of directed movement due to greater distances and incorrect bearings (see Bradshaw et al. 2007 for a large-scale case study). Indeed, our radio-tracking experiment conducted in the temperate forest showed even higher measurement error either in distance (4 m error) or bearings (72° error) than in the experiment with artificial trajectories due to the dense canopy and atmospheric interferences (we tracked beetles regardless of weather conditions from sunny days to rain). As a result, the trajectories recorded by a GPS device were notably different in shape than those recorded by distance-bearing.

For manual tracking, usually so-called ‘homing’ procedure is implemented (White & Garrott 1990). It requires being as close as possible to the tracked individual to record its exact position. Therefore, it should be noted that homing of ground-dwelling beetles can potentially increase the risk of crushing them under the foot or elicit their escape behaviour and consequently flawed recorded trajectories. There is no such disturbance in GPS transmitters. However, the lightest available GPS

tags weigh more than 3.5 g (Lotek Wireless Inc.) making these devices not eligible for tracking insect movement. To minimize the possible observer-induced disturbance, Riecken & Raths (1996) suggested stopping manual tracking at a 0.5 m distance from the expected signal source. Moreover, it is crucial to mention one potential computational bias by the software used for movement analyses that may also add extra error to the dataset. It seems the R package *AdehabitatLT* (Calenge et al. 2009) had a preset value for a minimum detected distance as 1.6 m. If the estimated distance is less than 1.6 m, the “as.ltraj” function automatically rounds it up to this value. Thus, it is not possible to estimate the movement distances less than 1.6 m.

In this study, we illustrated and discussed several issues of using a GPS device for recording movements of ground-dwelling beetles at the fine spatio-temporal scale. We can conclude that the distance-bearing method is more appropriate than GPS-established coordinates at the fine spatial scale. Although we used ground beetles as a model group, our findings can be relevant for tracking any walking species with limited dispersal power, from ground-dwelling arthropods to small vertebrates, such as frogs or lizards. The limitations in the precision of GPS units should be taken into account, especially in studies focused on microhabitat use. Although the distance-bearing method can be more time-consuming due to the manual record of each fix using a compass and a measuring tape, this method is more accurate and the derived movement parameters are more reliable.

5. Final remarks: What we can learn from studying ground beetles in fragmented forests?

Ground-dwelling predatory arthropods are among the best indicators for any habitat alterations in forested habitats. These groups have a short lifespan, have a higher position in the food web and give a complex response to changes in their abiotic and biotic environment. These groups give an ample example that evoking environmental filtering is often insufficient to explain assemblage responses. As we argued in above in chapters 2 and 3, environmental conditions determine assemblage composition not only directly via survival, but also by affecting biotic interactions. Ground beetles, a group with moderate mobility or dispersal power, gave weaker and somewhat less specific responses manifesting in a general decline in abundance. This is presumably caused by the short-term response of these invertebrates, which is explained by the loss of forest specialists due to either urbanisation or forest management. Ground beetles reacted positively to the canopy openness, where the higher species richness of ground beetles might be explained by the appearance of open-habitat species. Some recent findings revealed that functional diversity of ground beetles are not influenced only by the diversity of forest ground vegetation, other indirect drivers may occur (Elek et al. 2010, 2018, Koivula et al. 2019). Multiple ecosystem functions in forests require sets of species to form communities. Particularly in the light of global climate change scenarios, which predict more frequent disturbances and extreme weather events, it is important to explore the relationship between biodiversity and habitat alterations since the forest can be a tool for mitigation of climate change. Yet, the majority of researches on the impact of forestry on biodiversity has focused on a specific relationship between a certain management type and the response of a selected organism group. Although the results of this work do not provide direct evidence, I underline that dispersal dynamics may play a crucial role in the species-specific response to various forest management practices. The mobile ground-dwelling predatory arthropods, such as ground beetles, did not exhibit any easily interpretable mass effect, presumably due to their quick colonization by dispersal which enabled them to adapt to changes in the forest environment. In addition, there is still scarce information about the role of functional redundancy in intact forests (Elek et al. 2022). The majority of the published studies still emphasize the stabilizing function of high functional diversity for insect assemblages in habitat mosaics and only a few look for the clues behind this pattern (*sensu* Cadotte et al. 2013.). I assumed that the low functional diversity in control plots (i.e., closed forests) either in urbanised landscapes or in the (managed) forested landscape, suggesting that the available functional space, in terms of the ecological niche concept, is already held mainly by carnivorous forest specialist carabids with low dispersal capacity (Nolte et al. 2017). The

homogeneous closed forest habitats evidently have less spatial variation to host diverse functional skills for carabid assemblages, thus there is a spatial restriction for the available functional spaces which can drive the organisation of the assemblages. In addition, the relatively homogeneous forest stand with closed canopy can prevent the colonisation of opportunistic carabids and ensure the persistence of forest specialists, which provides the (functional) stability of forest ecosystems by environmental filtering.

There is still a huge knowledge gap about long-term perspectives of beetles' movement behaviour, especially in relation to population ecology and meta-community. Studies on the movement of beetles can be suitable for testing whether individual movement parameters help to understand community-level structures and changes (Grüm 1971a, b). The species composition, richness, and abundance (often called activity density in ground-dwelling arthropods) are frequently used characteristics of insect or beetle communities. The activity density is defined as the number of individuals that actively moved and were caught by a trap. This definition already gave a behavioural aspect to the interpretation as the activity of the individuals is positively correlated with the number of catches, suggesting a sort of habitat preference. Although this assumption seems to be logical at the first sight, there are several cases when it can be limited due to the demographic structure of local populations, species-specific movement activities or individual trajectory profiles (Grüm 1971a, b, Růžicková et al. 2021). Grüm (1971a, b) suggested that the differences in movement activity between individuals are based on their physiological condition (chances of food intake) and population density. These differences between trajectories can be explained by the behavioral aspect of the individuals due to their physiological condition (Grüm 1971a, b). The rate of metabolism can be linked to the population density, thus the movement probability will be higher in dense populations due to density-dependent movement behaviour. This increased mobility will be manifested in the increased rate of metabolism. Grüm (1971b) revealed that the directional movement between habitat patches can be the compensation of the dissimilarities in energy balance between individuals in the habitat mosaic. Moreover, an increased rate of mobility may lead to increased predation pressure (Grüm 1971b, Elek et al. 2021) that reduce the population density and may affect individual behaviour (Riecken & Raths 1996). Thus, the predator avoidance behaviour had an effect on the daily rhythm in the movement activity (Elek et al. 2021) as well as population density in habitat patches. All these clues may suggest that the individuals' perspective can be the manifestation of the inference of the physiological condition and the current state of the surrounding (micro)environment. Thus, these complex interactions of animals with their environment can be reflected in complex movement patterns suggesting that the individual responses can reflect a spectrum of decisions (Okuzaki 2021, Růžicková & Elek 2021a, b).

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