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Is the soil type an important ecological factor for occurrence of carrion beetles (Coleoptera: Silphidae)?

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Abstract. Carrion beetles (Coleoptera: Silphidae) ~~comprise an important and imperfectly understood part of Holarctic ecosystems. They~~ provide a valuable ecosystem service by promoting nutrient cycling and biological control of pests like noxious flies (Diptera: Calliphoridae and Sarcophagidae). Our main goal was to examine the relationship between the occurrence of carrion beetles and soil type. We studied 43,856 specimens of 15 carrion beetle species. They were obtained in 444 pitfall traps in the Czech Republic during 2009. We found that the abundance of seven carrion beetles – *Nicrophorus antennatus* (Reitter), *N. germanicus* (Linnaeus), *N. humator* (Gleditsch), *N. interruptus* (Stephens), *N. sepultor* (Charpentier), *Silpha obscura obscura* (Herbst) and *T. sinuatus* (Fabricius) – was significantly higher on chernozems or on fluvisols. These findings support our hypothesis that soil type could be is an important factor in the occurrence of necrophagous European carrion beetles. Our findings can be used in selecting important nature conservation sites (particularly inasmuch as *N. antennatus*, *N. germanicus* and *N. sepultor* are listed as endangered species on

the Czech Red List of Invertebrates) and especially localities on chernozems should be considered as potentially valuable. ~~and in forensic entomology.~~

INTRODUCTION

~~The majority of~~ Carrion beetles (Coleoptera: Silphidae) are obligate carrion feeders. They are frequently associated with the corpses of vertebrates and they provide a wide range of ecosystem services, such as to promote nutrient recycling and remove potential breeding sites of noxious flies (Diptera: Calliphoridae and Sarcophagidae), by effectively removing the corps (burying beetles – Nicrophorinae) or praying on fly larvae (Nicrophorinae and some Silphinae) (Anderson & Peck, 1985; Sikes, 2008; Goff, 2009).

Despite their relatively low global species diversity (186 species), they are widely spread over the Holarctic region (Sikes, 2008; Grebennikov & Newton, 2012).

Carrion beetles can be divided into two taxonomic groups, the subfamilies Silphinae and Nicrophorinae, which are morphologically and also ecologically different (Sikes, 2005). Burying beetles from the ~~subgenus-subfamily Nicrophorus (Fabricius)~~ (Nicrophorinae) are well known for their biparental care, while beetles from the subfamily Silphinae do not manifest such behavior (Peck & Anderson, 1985a; Sikes & Venables, 2013).

The phenology and habitat selection of carrion beetles have been intensively studied in recent years (e.g. Peck & Anderson, 1985b; Creighton *et al.*, 1993; Růžička, 1994; Lingafelter, 1995; Lomolino & Creighton, 1996; Kočárek, 2001; Archer, 2003; Hocking *et al.*, 2007; Mullins *et al.*, 2013). The relationship between soil characteristics and the occurrence of carrion beetles has also often been mentioned in the literature, but this has been based only on the authors' observations and without appropriate statistical testing (Pukowski, 1933; Paulian, 1946; Theodorides & Heerdt, 1952; Novák, 1961, 1962). The logical reason behind this hypothesis is that developmental cycle of many carrion beetles is tightly connected with soil. For example Nicrophorinae are burying corpses of small vertebrates for

[breeding and Silphinae pupate underground.](#) It has been proposed that a possible explanation for ~~this relationship~~[preferring one soil](#) could be that some soils are better able to maintain a stable environment in terms of moisture and temperature which is beneficial for the beetle populations (Novák, 1961, 1962). In a study of Nearctic insects, Looney *et al.* (2009) observed that deep, loess soils host more abundant populations of necrophagous beetles than do shallow rocky soils. They also found that some species actually prefer shallow rocky soils instead of deep, loess soils. This niche differentiation could be due to interspecies competition (Anderson, 1982a; Bishop *et al.*, 2002).

Detailed information about the biology of separate species can be used for the identification of important conservation sites of endangered carrion beetles as ~~(Jurzenski *et al.*; (2014) did for *Nicrophorus americanus* (Olivier) and also in forensic entomology (Bedick *et al.*, 1999; Anderson, 2010).~~

~~Beetles had been generally overlooked by forensic entomologists for a long time on the assumption that flies are able to locate a dead corpse much more quickly and therefore provide for a more accurate post mortem interval (PMI) (Midgley *et al.*, 2010). The work of Midgley & Villet (2009) challenged these assumptions when they found that the Afrotropical *Thanatophilus micans* (Fabricius) (Silphinae) is able to locate a carcass and start breeding within the first 24 hours, thus providing a PMI estimate similarly accurate as those based on flies. Also, because the beetles generally need a longer time to develop than do flies, they can be used in cases where the body is in an advanced stage of decomposition and flies are no longer present on the carcass (Midgley *et al.*, 2010).~~

Our field study is aimed at the habitat preferences of European open-landscape carrion beetles. Interspecies competition is discussed only in respect to other carrion beetles, because our trapping method was not directed to collecting other necrophagous invertebrates. We had expected that most species of the subgenus *Nicrophorus* would be more abundant on

chernozems than on fluvisols. Beetles from the subfamily Silphinae do not interact with soil as closely as do Nicrophorinae, and we therefore had no reason to think that their abundance would be different on chernozems or fluvisols.

MATERIAL AND METHODS

SITE SELECTION

Our study was conducted during 2009 in the Czech Republic in regions having a similar medium warm (MT10) to very warm (T4) climate (Cenia, [20152008](#)) and with similar occurrence of two different soil types (chernozems and fluvisols) in open-landscape habitats. In order to select suitable locations, we uploaded data on climate, soil type and land use from a Cenia ([20152008](#)) database into the geographical information system software ArcGIS 9.2 and looked for locations where these three conditions overlapped (ESRI, [20092008](#)). Accessibility was also taken into account.

We selected an equivalent number of locations on chernozems (33) and on fluvisols (33), which were clustered into three regions (see Fig. 1). These locations were at least 1.5 km apart, and we arranged them more or less while alternating linearly between sites on fluvisols and chernozems as on Fig. 2. A detailed description of the sites was published in Jakubec & Růžicka (2012).

TRAPPING

For collecting beetles, we used baited pitfall traps designed by Růžicka (2007), which were made from 1,080 ml plastic buckets (opening of 103 mm and 117 mm deep). These traps were filled with a mixed preservation solution of 200 ml water and 100 ml ethylene glycol. Traps were covered with a net of 2 cm mesh and an aluminum roof as protection against scavenging animals and washing out with rain. Frozen fish meat (codfish) and ripening cheese (Romadur)

98 were used as bait, placed in a small container (≈ 5 cm and 1.5 cm deep) and hung above the
99 preservation solution.

100 A line of five traps was placed at each location. The distance between these traps was at
101 least 20 m. They were placed within one continuous agricultural field, and no closer than
102 50 m from the edge of this biotope. The fields were selected as target habitat because soil
103 properties inside of such agricultural field are very homogenized and water regime is also
104 more stable than anywhere else, therefore it minimized the effect of extraneous confounding
105 variables.

106 These traps were exposed for two weeks during the main peaks of carrion beetle activity
107 (season): 17–31 May 2009 (spring), 5–19 July 2009 (summer) and 13–27 September 2009
108 (fall), based on data on activity from Růžicka (1994). The complete samples consists from
109 content of each trap over the these two week-week period periods. The samples were kept
110 stored separately and they were used in the analysis only if they could be considered as intact
111 (trap and bait was not disturbed or damaged by animals, humans or weather conditions);
112 which gave us some additional information about the seasonality of our carrion beetles.

113 Adult carrion beetles were identified to species level according to Růžicka & Schneider
114 (2004) and they were stored in 75% ethanol. Selected voucher specimens were dry mounted
115 and both are deposited in the author's collection.

116

117 DATA ANALYSIS

118 Detrended correspondence analysis (DCA) was performed on the species abundance data
119 from each locality to determine the length of the gradient and to detect whether some species
120 are co-varying.

121 To test the effect of environmental factors on carrion beetles we decided to use partial
122 canonical correspondence analysis (CCA) with the randomized block design where blocks

were defined by covariates (season and region). We chose CCA over RDA because DCA showed that length of gradient is more than 3.7 SD units long, therefore we had to use unimodal type of analysis. Bonferroni correction was applied to adjust for multiple comparisons of following environmental factors: **soil type** (chernozems and fluvisols), **climatic region** (warm – T2, very warm – T4 and mildly ~~warm~~–warm – MT10), **land cover** = crop (*Brassica napus*, *Beta vulgaris*, *Carthamus tinctorius*, *Glycine max*, *Heliantus annuus*, *Hordeum vulgare*, *Phacelia tanacetifolia*, *Triticum aestivum* and *Zea mays*) and their interactions. Influence of regions was filtered out by using it as covariate, because we were not interested in that effect.

The diversity of carrion beetles for each location and geographically related region was measured by calculating the Brillouin biodiversity index ($H = 1/N \cdot \ln(N!/n_1!n_2!\dots n_s!)$) from the total abundance data across all sampling periods (three times two weeks), where N is the total number of individuals at a location and n_1, n_2, \dots, n_s are the numbers of individuals of all carrion beetles collected at the location (Pielou, 1975). We used this index, because it does not assume randomness of sampling and equal attractiveness of traps as commonly used Shannon index (see Magurran, 2004). The number of specimens at each location was averaged over the number of samples, because they differed between the locations due to unavoidable adverse events (heavy washing out with rain or the destruction of entire trap).

We used the Wilcoxon rank-sum test with continuity correction to test our hypothesis that abundance of carrion beetles differ between studied soil types. This hypothesis was tested for the whole taxonomic family Silphidae and also for each individual species. We chose this nonparametric test because data did not approached normality. We also tested the effect of soil type on the Brillouin biodiversity index by Welch's t-test for two samples.

The significance level was set at 5%. Data management and all analysis was carried out using the ~~R statistical program~~ and Canoco 5 and R statistical program (ter Braak & Šmilauer, 2012; R Core Team, 2014).

RESULTS

In total, we obtained 444 intact samples of silphid communities from 39 different locations (18 on chernozems and 21 on fluvisols), the rest was destroyed or did not contain any carrion beetles. In these samples we found 43,856 specimens of 15 carrion beetle species (see Table 1). Three of them were listed on the Czech Red List of Invertebrates. *Nicrophorus antennatus* (Reitter) and *N. germanicus* (Linnaeus) are considered to be Endangered and *N. sepulchrorum* (Charpentier) is Nearly Endangered (Růžička, 2005).

The whole dataset was dominated by *Thanatophilus sinuatus* (Fabricius) (> 63% of total abundance). This species was also dominant in almost each season (>73% in spring and >58% in summer) except fall (12%) when it was moved to the third place by *Nicrophorus vespillo* (Linnaeus) (> 55%) and *Thanatophilus rugosus* (Linnaeus) (> 15%).

DCA showed that species did not cluster according to their percentage abundance on chernozems or fluvisols (see Fig 3). This suggested that more environmental factors could be involved. We tested all measured environmental factors used for CCA analysis, and the following ones came back as significant during the manual forward selection: soil type (chernozems ($p_{adj}=0.038$) and fluvisols ($p_{adj}=0.038$)) and three crops from land cover category (*Zea mays* ($p_{adj}=0.038$), *Hordeum vulgare* ($p_{adj}=0.038$) and *Helianthus annuus* ($p_{adj}=0.038$)) (see Fig 4). The remaining factors appeared to have no significant effect on composition of the carrion beetles in our study (climatic region (T4, T2 and MT10) and the rest of crops (*Brassica napus*, *Beta vulgaris*, *Carthamus tinctorius*, *Glycine max*, *Phacelia tanacetifolia* and *Triticum aestivum*)).

These finding led us to test the effect of soil on biodiversity and abundance of carrion beetles. The Brillouin biodiversity index ranged from 0.1884 to 1.271 between localities, but we did not confirm a significant relationship ($t=1.7472$, $p=0.09$), between this index and soil type (mean values of the Brillouin index: chernozems = 0.835 and fluvisols = 0.692).

~~We found significant relationship ($W=28677.5$, $p=0.001$) between studied soil types and abundance of carrion beetles.~~ The carrion beetles as a group were significantly more abundant on chernozems, median abundance equal to 62 ($SD = \pm 157.38$) than on fluvisols, median abundance equal to 37 ($SD = \pm 110.867$) ($W=28677.5$, $p>0.001$). We studied this phenomenon more closely on species level and we found that significantly higher number of specimens of the following species occurred on the chernozems: *Nicrophorus antennatus* ($W=26118.5$, $p>0.001$), *N. germanicus* ($W=25946.5$, $p=0.0288029$), *N. interruptus* (Stephens) ($W=26693$, $p=0.0296503$), *N. sepultor* ($W=31962$, $p>0.001$), *Silpha obscura obscura* (Linnaeus) ($W=31132$, $p>0.001$) and *T. sinuatus* ($W=28514.5$, $p=0.001$). Significant preference for the fluvisols was found only in the case of the *N. humator* (Gleditsch) ($W=23152.5$, $p=0.005$). For the rest of the species we did not find any significant relationship between their abundance and studied soil types, although we had to exclude some species from statistical evaluation altogether because they were underrepresented, namely: *N. investigator* (Zetterstedt) ($n=7$), *N. vespilloides* (Herbst) ($n=6$), *Oiceoptoma thoracicum* (Linnaeus) ($n=8$) and *Phosphuga atrata atrata* (Linnaeus) ($n=1$). For an overview of the results, see Fig 5 and Table 1.

DISCUSSION

During the field work we captured and identified 15 species of carrion beetles. Three of them are currently considered as rare and they are listed on the Czech Red List of Invertebrates as Endangered (*N. antennatus* and *N. germanicus*) or Nearly Endangered (*N.*

195 *sepultor*) (Růžička, 2005). The last ecological studies of these species in Europe were done
196 almost 50 years ago when they were probably much more common (Novák, 1966; Petruška,
197 1968). These species deserve much more attention, because they could play a major role in
198 the nature conservation as bio-indicators or umbrella species (see Guarisco, 1997; Holloway
199 & Schnell, 1997; Walker & Hoback, 2007; Creighton *et al.*, 2009; Crawford & Hoagland,
200 2010; Jurzenski *et al.*, 2014).

201 The most frequent species in the entire dataset was *T. sinuatus*. Its dominance was
202 overshadowed by *N. vespillo* and *T. rugosus*, but only during fall. All these species seems
203 very common in open landscape habitats and our findings confirmed old observations of
204 Novák (1962, 1965, 1966) and Petruška (1964).

205 *T. sinuatus* and *T. rugosus* were considered as co-occurring species without spatially or
206 temporally differentiated niche (Novák, 1966). The higher abundance of *T. rugosus* in
207 samples from fall could be explained as sign of temporal niche differentiation.

208 Some of the captured carrion beetles are considered to be forest species (*N. humator*, *N.*
209 *investigator*, *N. vespilloides* and *O. thoracicum*) by several authors (e.g. Růžička, 1994;
210 Kočárek & Benko, 1997). Although the traps were not directly associated with forest sites,
211 our observations are in line with their findings, because presence of these species in the
212 samples was mostly negligible (in total 32, 7, 6 and 6 specimens, respectively). The more
213 frequent occurrence of *N. humator* outside of forest was probably caused by higher flight
214 activity of this large and common beetle.

215 CCA analysis showed that the factors with the significant effect on species composition are
216 both soil types (chernozems and fluvisols) and three species of crops (*Zea mays*, *Hordeum*
217 *vulgare* and *Heliantus annus*). As you can see on the Fig 4, positions of these factors are
218 roughly orthogonal, with an exception of *H. vulgare* and *H. annus*, therefore they are
219 probably unrelated.

The relationship between all these crops and occurrence of the carrion beetles is very interesting. We think that it could be caused by the change of microclimatic conditions in fields. Based on our own experience, *Z. mays* is providing much more humid and cooler environment than *H. vulgare* and *H. annuus*. The further study is needed to reveal causality.

~~We were surprised that climatic region did not play any significant role according to the analysis. Climate is apparently not limiting factor in this case, but we tested only very narrow range of climatic regions (from very warm to mildly warm). Incorporating a wider range of climatic regions could yield different results.~~

We were able to show that abundance of seven carrion beetle species – *N. antennatus*, *N. germanicus*, *N. humator*, *N. interruptus*, *N. sepultor*, *Silpha obscura obscura*, and *T. sinuatus* – was significantly different on chernozems or on fluvisols, and we could therefore identify soil type as an important factor in the occurrence of these carrion beetles. Our findings are supported by results of CCA analysis and also Wilcoxon rank-sum tests.

This relationship had been assumed by many previous authors, but only for beetles from the subgenus *Nicrophorus* (e.g. Pukowski, 1933; Paulian, 1946; Theodorides & Heerdt, 1952; Novák, 1961, 1962). Heretofore, this phenomenon had been empirically proven only for North American species (Muths, 1991; Bishop *et al.*, 2002; Looney *et al.*, 2009) where the association of beetles from the subfamily Silphinae with a particular soil had previously been observed only by Bishop *et al.* (2002).

All these findings raise an important question as to what mechanisms drive such phenomenon. Muths (1991) had shown in a laboratory experiment that burying beetles are able to distinguish among different soil types and to choose the best substrate for digging. This experiment was conducted on a small scale (an area with a diameter of 1.5 m) and it is reasonable to think that this type of reaction occurs only during microhabitat selection. Thus, it cannot answer our question. Our goal was to address the issue if soil type could play an

important role in general habitat selection. Looney *et al.* (2009) offered three possible explanations. Beetles are either simply more abundant on one type of soil, or they preferentially colonize it, or they are more competitive on it. From our point of view the last option looks very likely and here are the reasons why.

We think that the one of the main driving forces in long range habitat selection by necrophagous carrion beetles is the presence of the food source (carrion) (Kalinová *et al.*, 2009). The higher abundance of these beetles on certain soil types (chernozems or fluvisols in our case) could be caused indirectly.

We know from population structure studies that burying beetles are good fliers and can cover long distances but that they mostly choose to stay closer to the original locations (e.g. *Nicrophorus americanus*, which is a relatively large and robust beetle, and is capable of flying as far as 7.41 km in a single night, but more typically it travels less than 1.6 km/night) (Jurzenski *et al.*, 2011). Limited mobility coupled with adaptation to local conditions could cause the observed spatial structure rather than individual habitat choice (preferential colonization). This is also in line with general local adaptation hypotheses (Alstad, 1998).

The same reasons can be applied to explain our finding in the case of *T. sinuatus*, because it has functional wings (Ikeda *et al.*, 2008), but only small flight range (Petrůška, 1964). Therefore, it has a very similar lifestyle as do the burying beetles under study: *N. antennatus*, *N. germanicus*, *N. humator*, *N. interruptus*, *N. investigator*, *N. sepultor*, *N. vespillo* and *N. vespilloides*. Our hypothesis is supported by the fact that all these species were found on both soil types and often in large numbers, so they are not closely associated with a certain soil type (see Table 1).

The biology of *Silpha obscura obscura* is not well known. The diet and flight ability of the whole genus *Silpha* is still in question (Ikeda *et al.*, 2007). There is also a strong possibility that this species is not strictly necrophagous. Its preference for chernozems is surprising in

this case, but it could be also explained by the spatial structure of the population, which is driven by the adaptation to conditions on chernozems.

Loess loams are proposed as preferred soils for many species of burying beetles (*N. antennatus*, *N. germanicus*, *N. interruptus*, *N. vespillo* and *N. sepultor*), but according to Novák (1962) *N. vestigator* should prefer sandy soils. This species is unfortunately not represented in our study despite the fact that we had traps near locations where it often had been observed by some collectors in the past. It is possible that we missed the population peaks of this rare species. Future study of this species should be focused on earlier months of the year (April–May) when it could be more abundant (Novák, 1962; Šustek, 1981).

Our findings are limited to the soil types under study (chernozems and fluvisols) and they can be extended only to similar soils (e.g. Phaeozems and haplic Luvisols). It is also possible that the distribution pattern of the studied species can shift throughout their distribution area, as has been pointed out by Scott (1998).

~~Knowledge as to the distribution of carrion beetles can be applied in forensic entomology. *T. rugosus* and *T. sinuatus* seem like the most promising species. Ridgeway *et al.* (2014) have proven that carrion beetles can be used to estimate PMI based on the example of Afrotropical *T. micans* and *T. mutilatus* (Castelneau), which are closely related species to our *T. rugosus* and *T. sinuatus*. The development of these species needs to be studied in more detail, but our understanding of their ecology and phenology is improving.~~

Thanks to our study we learned more about the distribution and ecology of European carrion beetles and especially about preferences of three endangered ones (*N. antennatus*, *N. germanicus* and *N. sepultor*) for chernozems (see also Jakubec & Růžicka, 2012). Our findings about possible adaptation driven soil type preferences of some carrion beetle species are crucial for the effective conservation of these species, which is an overlooked topic in the Czech Republic and in Europe generally. These beetles can be very charismatic and they can

become a widely accepted ~~umbrella-flagship~~ species for stakeholders and policymakers, as has been proven by the attention of public and vast number of studies on the American burying beetle (*N. americanus*) (e.g., Anderson, 1982b; Lomolino *et al.*, 1995; Amaral *et al.*, 1997; Crawford & Hoagland, 2010) ~~and we are obliged to take care of them as well.~~

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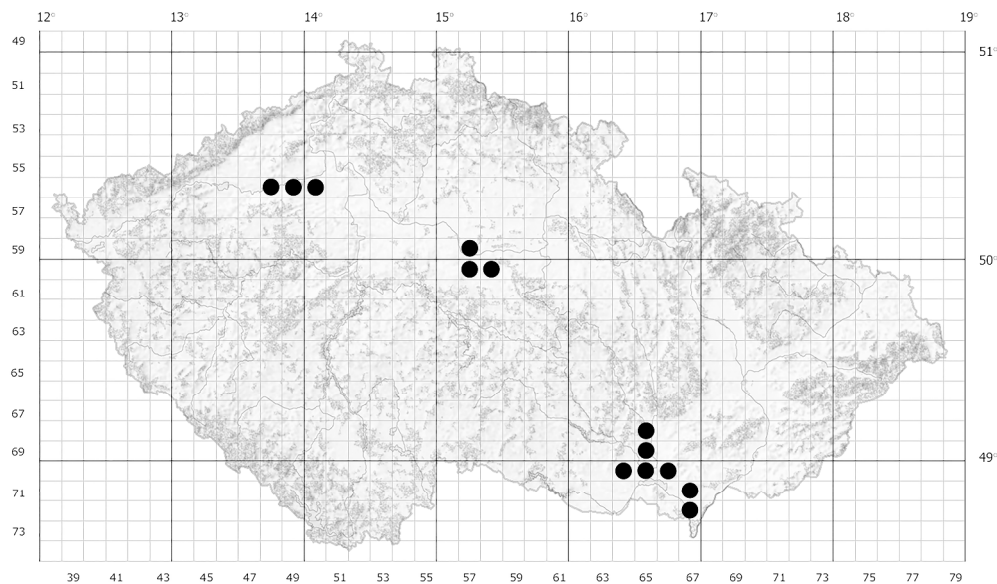


Fig 1. Study area within the Czech Republic, schematically represent by black dots on a faunistic grid map (Jakubec & Růžička, 2012).

505x298mm (300 x 300 DPI)

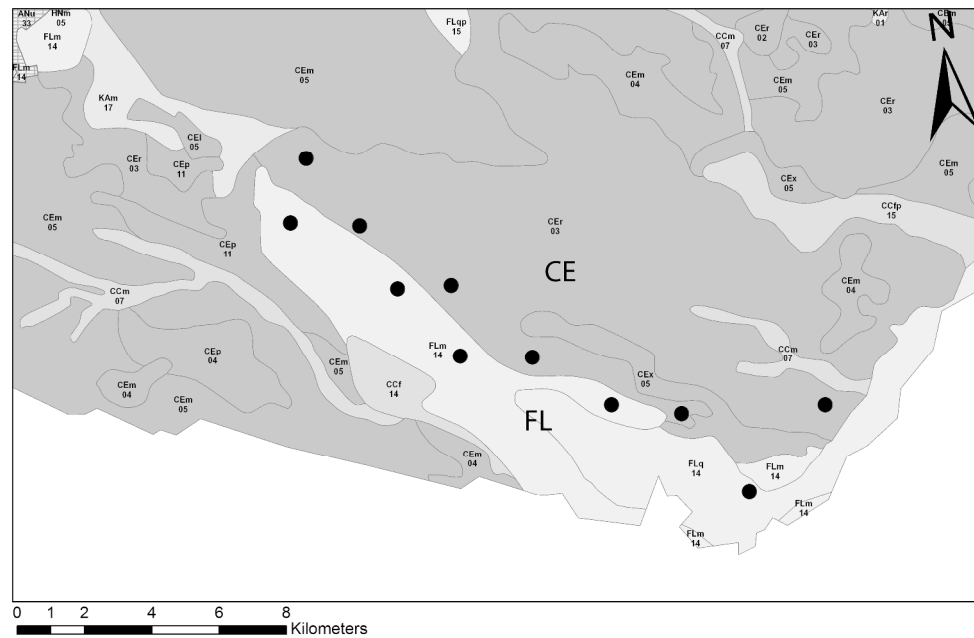


Fig 2. Distribution of the localities (black dots) based on the soil type (CE = czernozems; FL = fluvisols) in the South Moravia region (Cenia, 2015).
297x210mm (300 x 300 DPI)

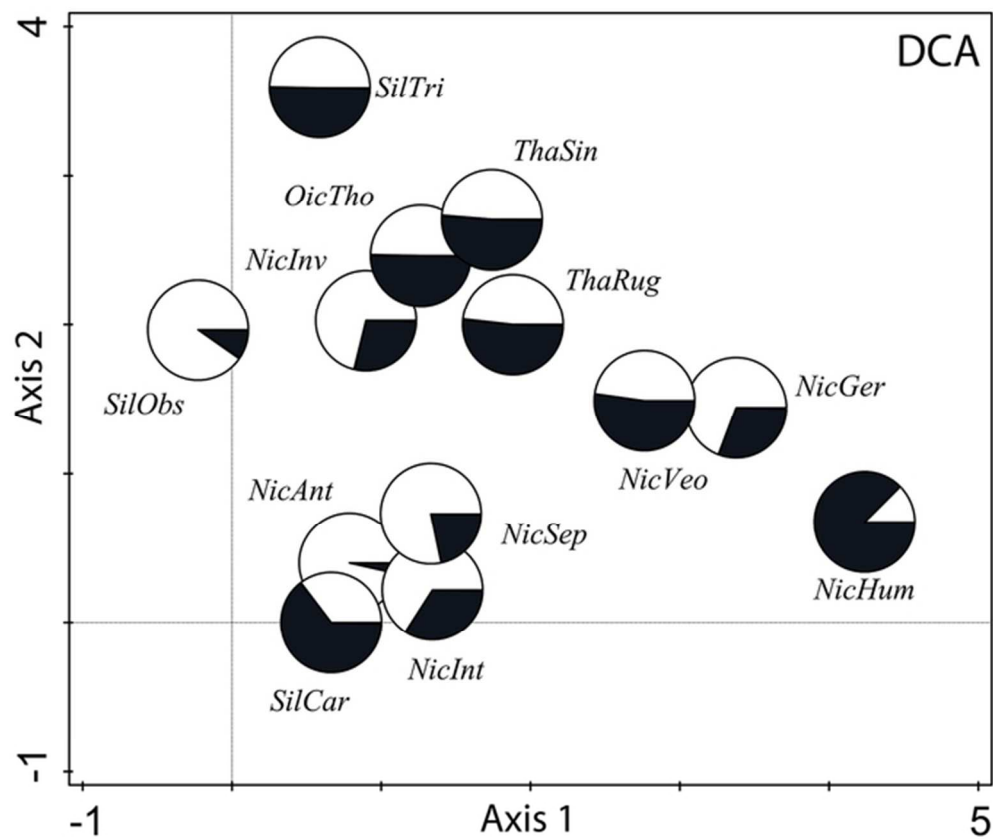


Fig 3. Unconstrained DCA of all species (*NicAnt* = *N. antennatus*; *NicGer* = *N. germanicus*; *NicHum* = *N. humator*; *NicInt* = *N. interruptus*; *NicInv* = *N. investigator*; *NicSep* = *N. sepultor*; *NicVeo* = *N. vespillo*; *NicVes* = *N. vespilloides*; *OicTho* = *O. thoracicum*; *SilCar* = *S. carinata*; *SilObs* = *S. obscura obscura*; *SilTri* = *S. tristis*; *ThaRug* = *T. rugosus*; *ThaSin* = *T. sinuatus*) with their percentage abundance on different soil types (chernozems – black, fluvisols – white) illustrated by pie charts.
58x49mm (300 x 300 DPI)

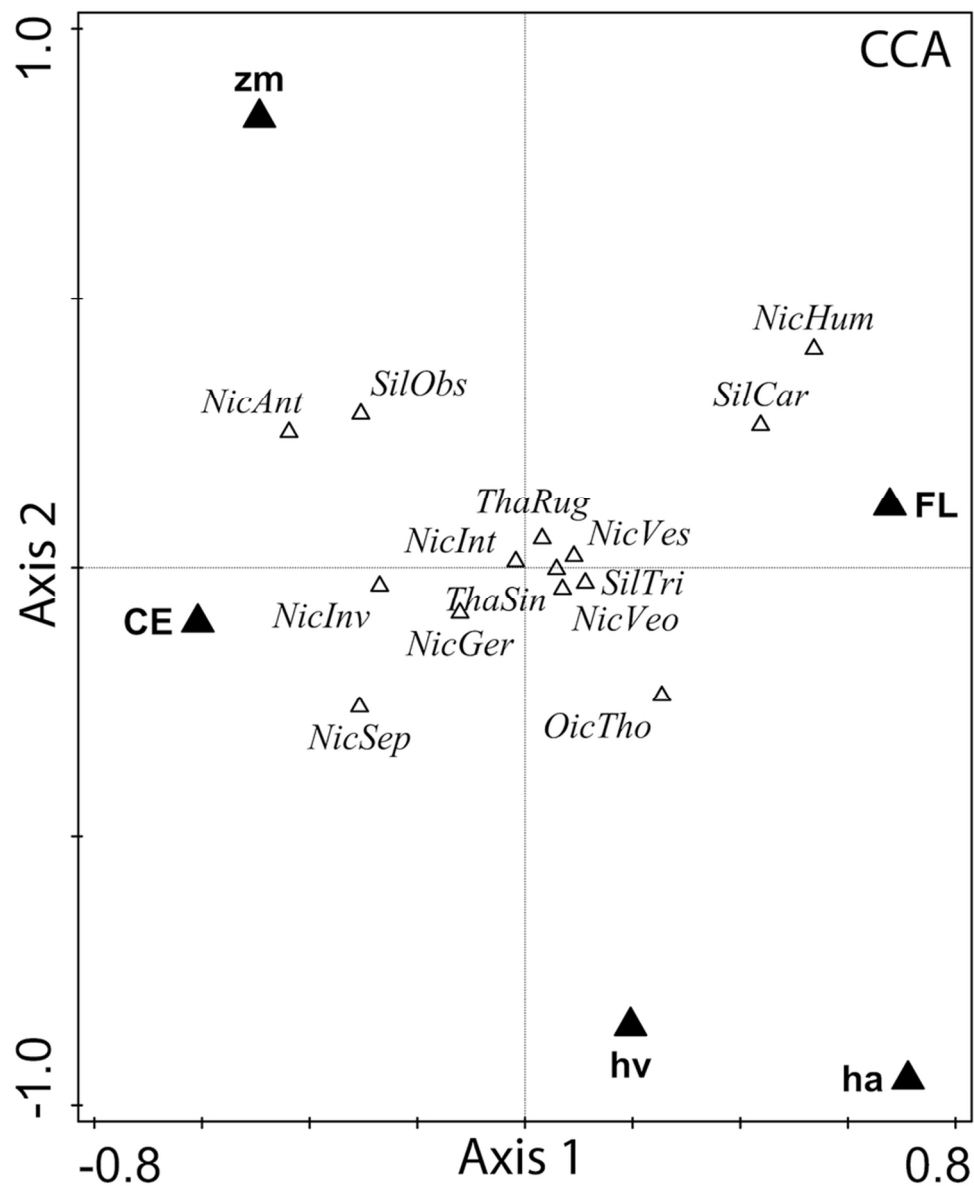


Fig 4. Partial CCA ordination diagram with carrion beetles and statistically significant environmental variables (CE – chernozems, FL – fluvisols, zm – Zea mays, hv – Hordeum vulgare, ha – Heliantus annus).
81x97mm (300 x 300 DPI)

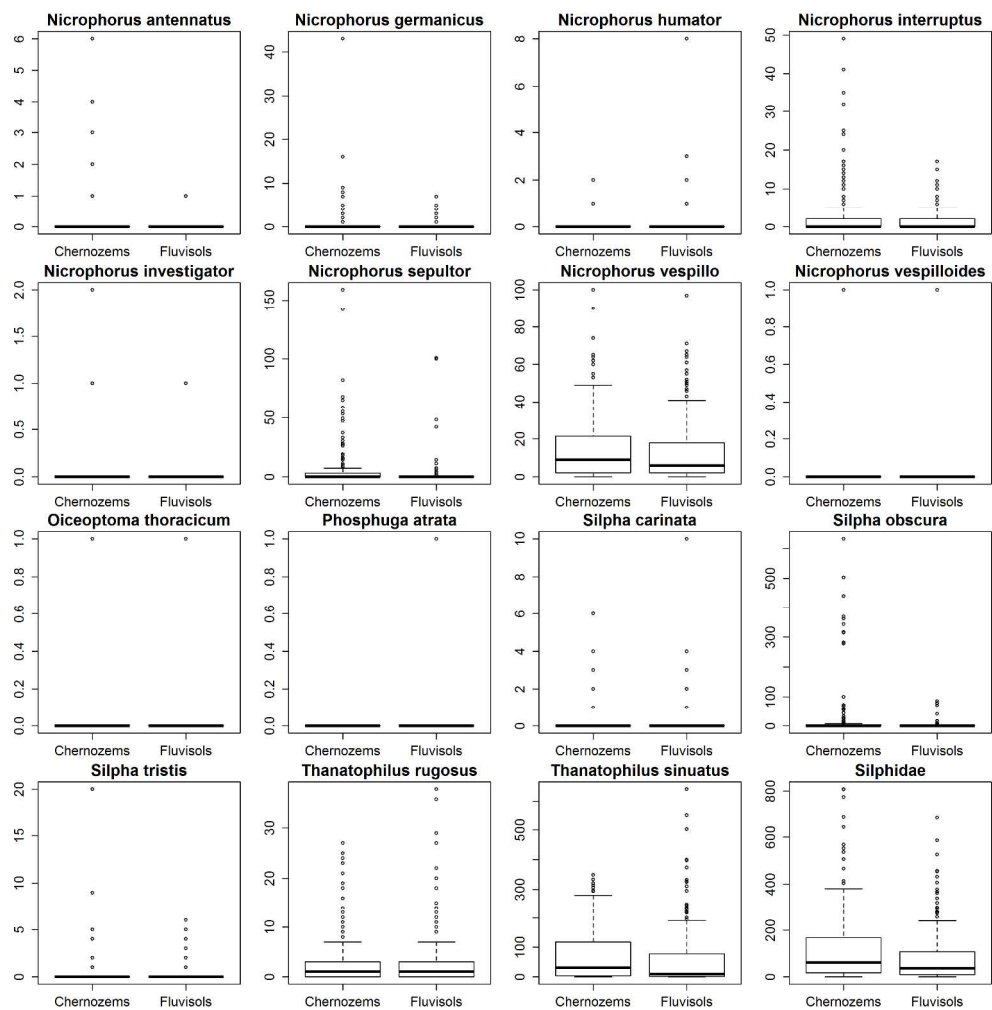


Fig 5. Box plots of all observed carrion beetles on two soil types. The thick horizontal lines within the boxes show median values. The upper and lower boxes show the 75th and 25th percentiles, respectively. Whiskers show values within the 1.5 interquartile ranges. Small circles are outliers.
279x279mm (300 x 300 DPI)