Macrohabitat associations and phenology of Carrion Beetles (Coleoptera: Silphidae, Leiodidae: Cholevinae)

Authors details

Matthew Esh*, Anne Oxbrough

Biosciences Building, Edge Hill University, St Helens Road, Ormskirk, Lancashire, L39 4QP

*mattesh123@hotmail.co.uk

Abstract

1. As decomposers of vertebrate carcasses, carrion beetles (Coleoptera: Silphidae, Leiodidae: Cholevinae) play a significant role in the functioning of terrestrial ecosystems. Despite this, the ecology and phenology of this group is relatively understudied. This research determines carrion beetle assemblages in three macrohabitats - native broadleaf woodland, non-native coniferous plantations and unforested sites of grassland or heathland. Further, it explores phenological changes over the growing season.
2. Each macrohabitat type was replicated in eight geographical clusters, giving a total of 24 sites. Clusters were selected to give a wide geographical spread across Britain. Six pitfalls were set at each site, three baited with mice and three with cheese. Traps were set and collected fortnightly within every month from May to September 2016.
3. The taxa differed in response to macrohabitat and growing season. Silphidae assemblages differed between forested and unforested habitats, whereas Leiodidae: Cholevinae were not distinguished by macrohabitat, although some specialists of forests were identified.
4. Silphidae assemblages differed over the growing season, with May and June supporting a different suite of species to those in July - September. In contrast, Leiodidae: Cholevinae assemblages changed very little over the growing season though some species did prefer particular time periods.
5. This research presents the first large-scale study of the macrohabitat preference and phenology of carrion beetles in Western Europe, providing important ecological and phenological information which could aid in their conservation.

Keywords: Silphidae, Leiodidae: Cholevinae, carrion, habitat preference, phenology

Declarations – Not applicable

Introduction

Carrion beetles play an important role in the functioning of terrestrial ecosystems as decomposers of vertebrate carcasses, a key element of the nutrient cycle (Kočárek, 2003). During this process, constituent components of carrion leach into the soil, facilitating nutrient release (Farwig et al, 2014). For instance, the increased nitrogen released in the microhabitat around a decomposing carcass enhances soil fertility and stimulates biomass production (Towne ,2000). Through feeding and reproduction, carrion insects play a role in dispersing these nutrients (Barton et al., 2013). Together, these actions can directly affect decomposition rates (Pechal et al., 2014), and these can be altered by specific species of carrion beetle (Farwig et al., 2014). Therefore, knowledge of the ecology of this important group will provide a basis for the understanding of the role they play in ecosystem functioning.

Carrion beetles have been relatively well-studied in some contexts. For instance, the Silphidae subfamily, Nicrophorinae, have been extensively researched as they exhibit bi-parental care, an unusual behaviour in the invertebrate world (Dekeirsschieter et al., 2011). Yet, despite their importance to ecosystem functioning, less research has explored the ecology of carrion beetles. Several studies in Europe have found species specialise between forested and unforested habitats (Kočárek, 2001, Růžička, 1994), high forest cover and forest clearings (Peschke et al., 1987) or moist and shaded habitats (Peck & Cook, 2002). These differences have been attributed to a variety of factors including differences in soil types, moisture and ground vegetation (Kočárek, 2001, Růžička, 1994, Peck & Cook, 2002, Peschke et al., 1987) and being driven by presence of food resources or microclimate tolerances. Further, research has explored carrion beetle phenology, finding differences in carrion beetle activity across the growing season (Chandler & Peck, 1992; Peck & Anderson, 1985; Růžička, 1994). Seasonal preferences of species are linked to the number of broods produced per year and avoidance of competition between species (Růžička 1994; Kočárek, 2001). However, despite these handful of studies in North America and Eastern Europe, the ecology of many carrion beetles, particularly in western European temperate habitats, remains understudied.

Carrion beetles are likely to be affected by key environmental changes which are impacting biodiversity across the globe. Carrion is an ephemeral resource, and organisms which require it for feeding and reproduction are likely to be negatively affected by habitat loss and fragmentation, since they must travel greater distances to find it, putting them at increased risk of mortality (Gibbs & Stanton, 2001). Further, increasing intensity of land use and changing climate conditions (e.g. through higher ambient temperatures) has been shown to negatively affect carrion beetle abundance (von Hoermann et al., 2018). By directly altering beetle communities, these increasingly profound environmental changes may ultimately impact the role they play in the nutrient cycle. Therefore, a better understanding of carrion beetle ecology is crucial, in order to begin to understand how to maintain the ecosystem functions associated with carrion beetle decomposition. We aim to address this by providing the first large-scale study of carrion beetle macrohabitat preferences and phenology in western Europe. Specifically, it will determine how three common macrohabitat types (broadleaved woodland, conifer plantation forest and unforested open habitats) affect carrion beetle assemblages and it will identify how these assemblages change across the growing season.

In this study we explored two beetle taxa, the Silphidae family (Silphids) and the Cholevinae tribe (Cholevids) from the Leiodidae family. Silphids are medium to large (9-30mm) beetles, frequently found on small mammal or bird carcasses, and include the burying beetle subfamily *Nicrophorinae*. They find carrion using sensitive chemosensors (Scott, 1998), often flying several kilometres to find the carcass (Kalinová et al., 2009). Cholevids are small to minute beetles (1-7mm), and are generalist detritivores, consuming decomposing leaf litter, carrion & fungi (Tizado & Salgado, 2000). They are attracted to any size of decomposing carrion, feeding *in-situ*, and very little is known about how they find this decaying material. By studying these two very different carrion beetle groups, which have contrasting ecological requirements, we will gain a broader understanding of carrion beetle ecology, aiding in the conservation of these beetles.

Materials and Methods

Study Sites –

Three habitats were selected for study to represent major macrohabitat types, these were broadleaf woodland, conifer plantation and unforested habitats of grassland or heathland (Table 1). These were selected since they differ significantly in microclimate, soil and litter, and ground vegetation, factors known to affect carrion beetle communities (Kočárek, 2001, Růžička, 1994, Peck & Cook, 2002 Peschke et al., 1987). Broadleaf woodlands were defined as a continuously wooded area since 1900 from historical online maps (https://www.old-maps.co.uk/#/) and dominated by native broadleaf species such as Oak (*Quercus sp*.) & Alder (*Alnus sp*.). Conifer plantations were commercially mature Norway spruce *(Picea abies*, L. Karst), Sitka spruce (*Picea sitchensis*, Bong, Carr), Corsican pine *(Pinus nigra*, Laricio) or Scots pine *(Pinus sylvestris*, Linnaeus). The conifer sites were planted between 1961 to 1975. Unforested macrohabitats were chosen to be in close vicinity to the forested sites and which were semi-natural in management approach rather than intensive agriculture. These included upland acid grassland, lowland pasture, lowland heathland and recovering heathland according to Hawley et al., (2008). Forest of Dean contains recovering heathland, this was previously a coniferous forest that was cleared in 1981 and allowed to return to heathland.

Each macrohabitat type was replicated in eight geographical clusters, giving a total of 24 sites. Clusters were selected to give a countrywide spread across England and into Wales (Figure 1). To ensure that sites within a cluster had access to the same regional species pool they were always within 12 km of each other (mean distance 4km ±3 SD). Sites within a cluster were matched for elevation and soil type where possible. Mean variation in elevation within a cluster was 39m ±30 SD. However, at Grizedale the broadleaf woodland plot was at 67m and the conifer woodland plot at 208m. Furthermore, at Grizedale, the conifer and unforested sites were on peat while the broadleaf woodland was loam, and in Gisburn the unforested site was peat while the others were on loam.

Table 1 Description and location of sites used in study

Site	Macrohabitat type	Habitat details	Elevation (m)	Lat/Long	Soil Type
Pembroke	Broadleaf	Oak	49	49° 89'-7° 50	Loam
	Conifer	Norway Spruce	95	49°89′-7° 45	Loam
	Unforested	Lowland Pasture	105	49°87′-7° 43	Loam
Forest of Dean	Broadleaf	Oak	96	49°84′-6° 70	Loam
	Conifer	Sitka Spruce	140	49°84′-6°71	Loam
	Unforested	Recovering Lowland Heathland (Hawley et al., 2008)	191	49°92′-6°69	Loam
Alice Holt	Broadleaf	Oak	82	50°17′-6°46	Loam
	Conifer	Corsican Pine	106	50°18′-6°46	Loam
	Unforested	Lowland Heathland	66	50°18′-6°40	Sand
Thetford	Broadleaf	Oak	69	50°42′-7°59	Loam
	Conifer	Scots Pine	39	50°60′-6°33	Sand
	Unforested	Lowland Heathland	45	50°59′-6°35	Sand
Sherwood	Broadleaf	Oak	76	50°41′-6°75	Sand
	Conifer	Corsican Pine	83	50°41′-6°78	Sand
	Unforested	Lowland Heathland	59	50°42′-6°76	Sand
Cannock	Broadleaf	Oak	138	50°00′-6°20	Sand
	Conifer	Corsican Pine	179	49°99′-6°19	Sand
	Unforested	Lowland Heathland	143	49°99′-6°22	Sand
Grizedale	Broadleaf	Oak	67	50°31′-6°57	Loam
	Conifer	Norway Spruce	208	50°33′-6°56	Peat
	Unforested	Upland Acid Grassland	186	50°31′-6°57	Peat
Gisburn	Broadleaf	Alder	211	50°59′-7°17	Loam
	Conifer	Norway Spruce	270	50°65′-7°17	Loam
	Unforested	Upland Acid Grassland	225	50°64′-7°21	Peat

Beetle Sampling–

At each site, a sampling plot was established at least 50m away from the edge of the site and in an area typical of the habitat, avoiding disturbance such as paths. In the plot six baited pitfalls traps were set in a line, with traps arranged 2m apart. Pitfall traps were used to sample carrion beetles. These were 11cm deep and 8cm in diameter, with 50% propylene glycol solution added to a depth of 2cm. Two different baits were used - decomposing mouse carcass, which is an efficient attractant of a range of carrion beetles (Rintoul et al., 2005), and, decomposing cheese. Decomposing cheese is a commonly used bait for Cholevids (Růžička, 1994), likely attracting them through sulphur-containing volatile organic compounds (Kalinová et al., 2009). Three pitfalls were baited with a whole mouse carcass and three with a cube of cheese, with baits alternated along the line of six traps. Baits were aged for one week prior to deployment.

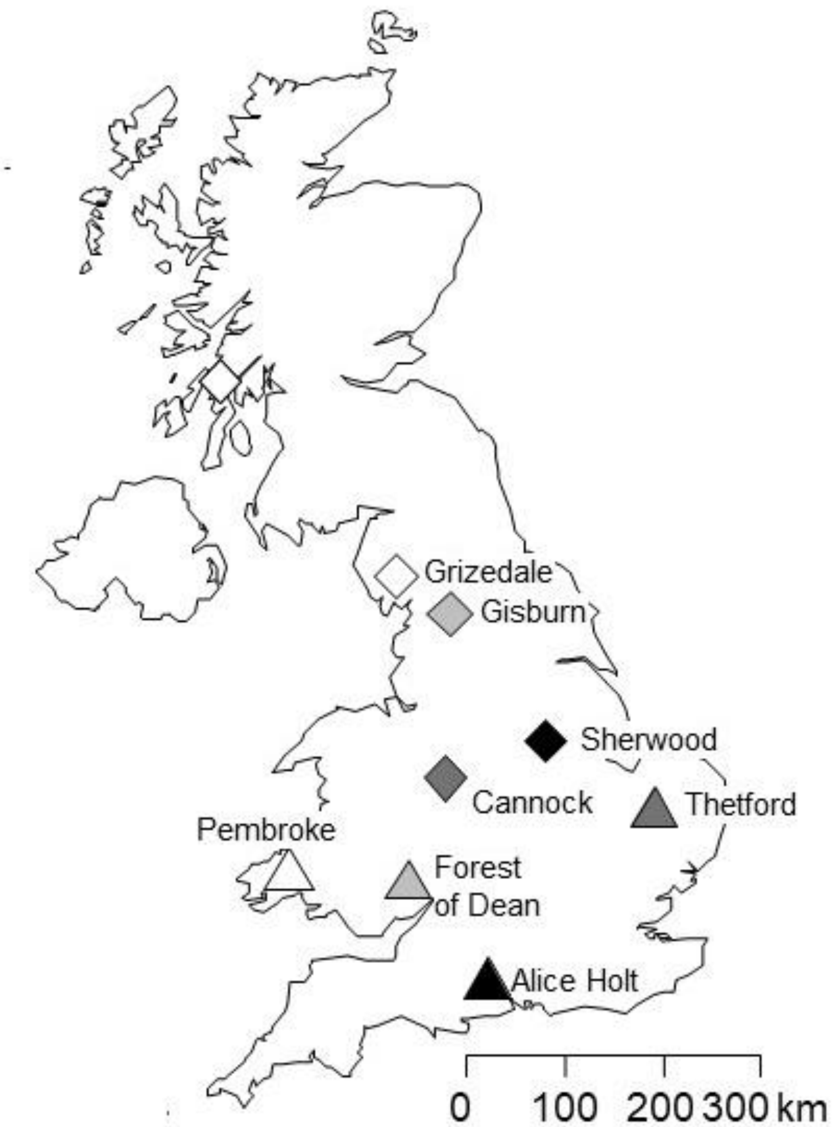


Fig. 1 Map of site clusters across the UK. Each cluster contains one deciduous woodland, one conifer forest and one unforested

Each bait was wrapped in mosquito netting as a fly deterrent and with some copper tape wrapped around to deter slugs (Supplementary Material 1). Baits were hung over the trap, and the whole construction was covered with a metal cage (mesh size 2.5x2.5cm) to deter mammals and birds from disturbing the bait. Traps were set and collected fortnightly within every month from May until September 2016, giving 70 trapping days across the main activity period (Růžička, 1994). March and April trapping periods were included in the original sampling design, but the catch was zero and so these months have been excluded from the analyses. Silphids were identified to species using Wright (2009) and Cholevids were identified to species using Duff (2012). The conservation status of species captured was checked on the UK's Natural History Museum website (Natural History Museum, 1999) which contains the most up to date species status information for Coleoptera.

Data Analysis –

For all analyses, data were pooled by each bait type (e.g. 3 traps per type) and each beetle family were analysed separately. The Sherwood unforested site and Forest of Dean conifer site lost one set of fortnightly samples, giving a total of 56 trapping days. The Alice Holt unforested site had significant losses giving a total of 28 trapping days. Across sites the data was standardised by dividing the number of individuals in each species by the number of trapping days at that site and multiplying it by the maximum number of trapping days (70) across all sites, following Lyons et al. (2017). All analyses were carried out using the statistical programme R (version 3.2.0) (R Development Core Team, 2016).

To determine whether carrion beetle diversity differed by macrohabitat type data were pooled across the growing season. To determine if species richness and number of individuals captured in the sample (hereafter termed abundance) differed by macrohabitat Generalised linear mixed modelling (GLMM) was performed. GLMMs assumed a poisson distribution (for count data), with macrohabitat type as the fixed factor and geographic cluster as the random factor. This was carried out using the 'glmer' function of the lme4 package (Bates et al., 2015). Significance was tested using the 'Anova' function of the carr package (Fox & Weisburg, 2011), and when significant, Tukey post hoc tests were carried out using the Holm method using the 'glht' function of the multcomp package (Hothorn et al., 2008).

Carrion beetle assemblages among macrohabitats were analysed using Redundancy Analysis (RDA), performed with the 'rda' function in the vegan package (Oksanen et al., 2016). The data were Hellinger transformed prior to analysis. Cluster was included as a conditional variable, however, a fixed factor was not specified in the model, and so the resulting 'RDA' can be interpreted as an unconstrained Principal Component Analysis in which the variation attributed to geographical location was removed. From the RDA, groups were distinguished, and Indicator Species Analysis was carried out on these to determine significant macrohabitat associations of carrion beetles. This analysis used the 'indval' function of the labdsv package (Roberts, 2015). Indicator Species Analyses provides a value between 1 and 0, with a value of 1 allocated to a species with high relative abundance and frequency in that *a-priori* group relative to the others. This value is tested for significance with Monte Carlo permutations.

To determine whether carrion beetle diversity differed by growing season, data were pooled across the macrohabitats. To determine if species richness and abundance differed across the growing season, GLMMs were performed as previously described, with month as the fixed factor and geographic cluster as the random factor. Change in carrion beetle assemblages across growing season were analysed using Principal Component Analyses carried out on Hellinger transformed assemblage data with cluster as a conditional variable as previously described. Finally, phenological trends in the abundance of the most common species were explored graphically. Common species were defined as those with over 100 individuals collected, as this gives a random chance of each of the five months supporting 20 individuals. This was considered a robust number on which to draw conclusions on phenological trends.

Results

In total 12,539 individuals were collected during the study with 6578 Silphids from eight species and 5961 Cholevids from 17 species (Table 2). The Silphid catch was dominated by *Nicrophorus vespilloides* with 4750 individuals (72% of the catch). Six specimens of *Nicrophorus interruptus* were captured. This species is designated Nationally Scarce in the UK, having been recorded in only 30-100 10km squares). *N. interruptus* specimens were found in three sites, with 4 out of 6 specimens coming from the broadleaf woodland in Thetford, the other two from the broadleaf woodland and the unforested habitat at Alice Holt. The Cholevid catch was dominated by *Sciodrepoides watsoni* with 2016 individuals (34%) and *Catops morio* with 1794 (30%). 43 specimens of *Catops longulus* were captured. This species is designated Nationally Scarce in the UK, having been recorded in only 16 - 100 10km squares. It was found in all site clusters in small numbers, however most frequently in forested macrohabitats (35 specimens). It was most abundant in the broadleaf woodland in Cannock with 6 specimens.

Table 2 Number of individuals captured (catch) and the percentage they contributed to the total captures, for each beetle family

Family/Species	**Catch**	**Percentage catch**
Silphidae		
Nicrophorus vespilloides (Herbst, 1783) *	4750	72.2%
Nicrophorus vespillo (Linnaeus, 1758) *	416	6.3%
Nicrophorus humator (Gleditsch, 1767) *	128	1.9%
Nicrophorus investigator (Zetterstedt, 1824) *	192	2.9%
Nicrophorus interruptus (Stephens, 1830)	6	0.1%
Phosphuga atrata (Linnaeus, 1758)	83	1.3%
Thanatophilus sinuatus (Fabricius, 1775) *	569	8.7%
Thanatophilus rugosus (Linnaeus, 1758) *	219	3.3%
Oiceoptoma thoracicum (Linnaeus, 1758) *	215	3.3%
Total	6578	
Leiodidae		
Sciodrepoides watsoni (Spence, 1813) *	2016	33.8%
Sciodrepoides fumatus (Spence, 1813) *	671	11.3%
Catops morio (Fabricius, 1787) *	1794	30.1%
Catops grandicollis (Erichson, 1837)	84	1.4%
Catops fuscus (Panzer, 1794) *	350	5.9%
Catops coracinus (Kellner, 1846) *	308	5.2%
Catops kirbii (Spence, 1813)	73	1.2%
Catops tristis (Panzer, 1793) *	371	6.2%
Catops longulus (Kellner, 1846)	43	0.7%
Catops nigrita (Erichson, 1837)	18	0.3%
Catops chrysomeloides (Panzer, 1798)	9	0.2%
Catops fulginosus (Erichson, 1837)	34	0.6%
Nargus velox (Spence, 1813)	59	1.0%
Choleva lederiana (Reitter, 1902)	52	0.9%
Choleva agilis (Illiger, 1798)	78	1.3%
Choleva glauca (Britten, 1918)	1	<0.1
Total	5961	

*Abundance species included in individual analyses

Carrion beetle macrohabitat associations -

Silphidae species richness was similar among macrohabitats ($X^2_{df=2}$ = 0.89, p= 0.20) (Figure 2). In contrast, for Cholevids it differed significantly ($X^2_{df=2}$= 6.37, p= <0.001), where both forested macrohabitats had significantly more species than unforested (Figure 2). Silphidae abundance differed among habitats ($X^2_{df=2}$ = 162.46 p=<0.0001) with unforested habitats supporting greater abundance than forested habitats (Figure 2). In contrast, Cholevid abundance was greater in forested habitats compared to unforested habitats ($X^2_{df=2}$ = 400.55, p=<0.0001) (Figure 2). There was no difference between broadleaf and conifer forests for either carrion beetle group.

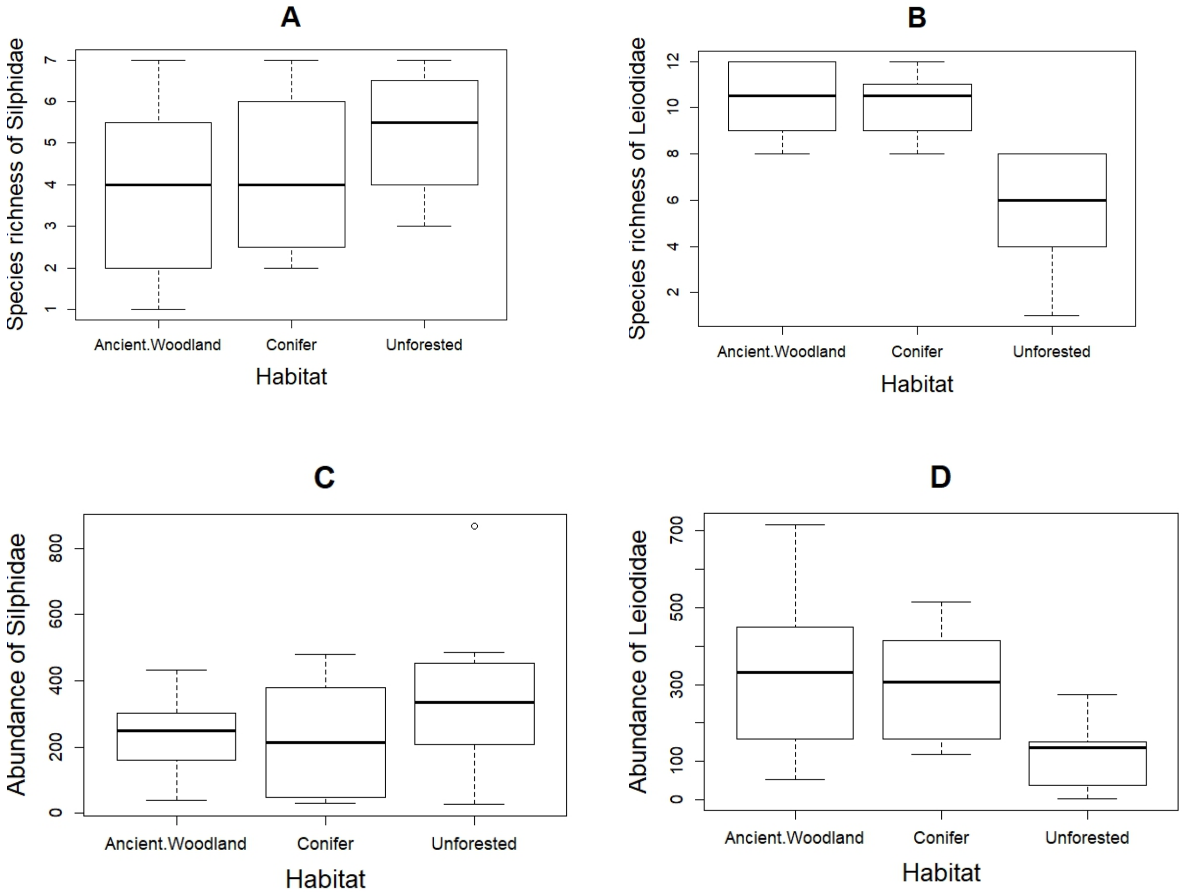


Figure 2 Species richness (a, b) and abundance (c, d) of Silphidae and Leiodidae among the macrohabitats

The RDA of assemblages for Silphids represented 73% of variation in the data, with 14% accounted for by the conditional variable, cluster location. Overall, there was a separation of assemblages between forested and unforested macrohabitats for Silphidae beetles (Figure 3a). However, the plantation and woodland forested habitats did not support distinct assemblages and two of the unforested sites (Gisburn and Grizedale) were similar to the forested sites in assemblage structure (Figure 3a). In general, the unforested habitats had greater variation in assemblages, in comparison with the forested sites. The RDA analyses of assemblages for Cholevids represented 47% of variation in the data, with 15% accounted for by cluster location. There was no distinction of assemblages by habitat type (Figure 3b), with all displaying similar levels of spread across the ordination space.

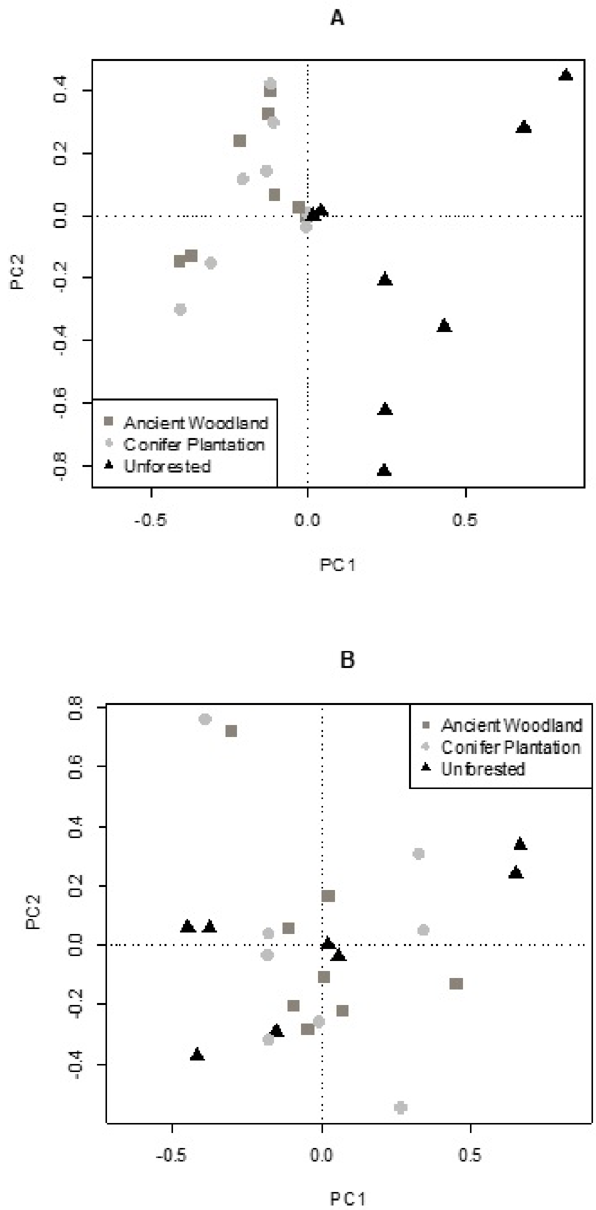


Figure 3 Redundancy analysis (conditional on cluster location) of Silphidae (A) and Leiodidae (B) assemblages among the macrohabitat types (A, PC1 = 73%, PC2 = 13%; B, PC1 = 47%, PC2 = 15%)

As the PCA of Silphids indicated a major distinction of assemblages between forested and unforested habitats, these were used as ecologically meaningful *a priori* groupings in the Indicator Species Analysis (Table 3). For consistency, the same was done for Cholevids (Table 3). This analysis revealed that *N. vespilloides* & *Phosphuga atrata* are significantly associated with forested habitats and *Thanatophilus rugosus*, *Thanatophilus sinuatus* & *Nicrophorus vespillo* are significantly associated with unforested habitats. For Cholevids there are nine species strongly associated with forested habitats while none are associated specifically with unforested habitats.

Table 3 Species of Silphidae and Leiodidae: Cholevinae with significant indicator values for either forested or unforested macrohabitats

Species	**Macrohabitat**	**Indicator value**	**Probability**
	Silphidae		
Phosphuga atrata	Forested	0.6867	0.026
Nicrophorus vespilloides	Forested	0.6859	0.02
Thanatophilus rugosus	Unforested	0.863	0.004
Nicrophorus vespillo	Unforested	0.7356	0.019
Thanatophilus sinuatus	Unforested	0.625	0.035
	Leiodidae		
Sciodrepoides fumatus	Forested	0.9821	0.001
Catops tristis	Forested	0.9784	0.002
Catops coracinus	Forested	0.9578	0.001
Catops fuscus	Forested	0.9543	0.001
Catops morio	Forested	0.8881	0.003
Catops nigrita	Forested	0.8750	0.002
Nargus velox	Forested	0.8750	0.001
Catops grandicollis	Forested	0.7500	0.031
Catops longulus	Forested	0.7122	0.031

Carrion beetle phenological trends across the growing season -

Both Silphid and Cholevid species richness was similar across the growing season ($X^2_{df=4}$= 0.93, p= 0.23 and $X^2_{df=4}$ = 1.50, p= 0.37 respectively) (Figure 4). Similarly, Silphid and Cholevid abundance did not change across the growing season ($X^2_{df=4}$ =102.55 p=0.26 and $X^2_{df=4}$ = 26.25, p=0.66 respectively) (Figure 4).

Overall, there was some separation of assemblage between month across the growing season for Silphids (Figure 5A). May and June are distinguished from the other months, variation between month accounted for 70% of the variation with cluster accounting for 30%. In contrast, Cholevid beetle assemblages show no distinct patterns by sampling period (Figure 5B) with month accounting for 8% of the variation and cluster 92%.

Of the common Silphids, *N. vespilloides* & *N. vespillo* are both active throughout the growing season (Figure 6 A, B). *Nicrophorus investigator* is active late in the growing season with few to no specimens collected in May and June respectively (Figure 6C) while *Nicrophorus humator* is active early and late in the growing season (Figure 6D). Both *T. sinuatus* and *T. rugosus* are most active midway through the growing season, in July and August (Figure 6E, F). Finally, *Oiceoptoma thoracicum* has a bimodal distribution, with one peak in May and the other in August (Figure 6G).

Of the common Cholevids, *S. watsoni* has lowest activity in June and September (Figure 7A). While *C. morio* has a peak of activity in June (Figure 7C). *Catops coracinus* peaks in activity in May (Figure 7D). Figure 7B & 7F show *Catops tristis* and *Sciodrepoides fumatus* have highest activity in May and June whereas *Catops fuscus* prefers mid-summer from June to August (Figure 7E).

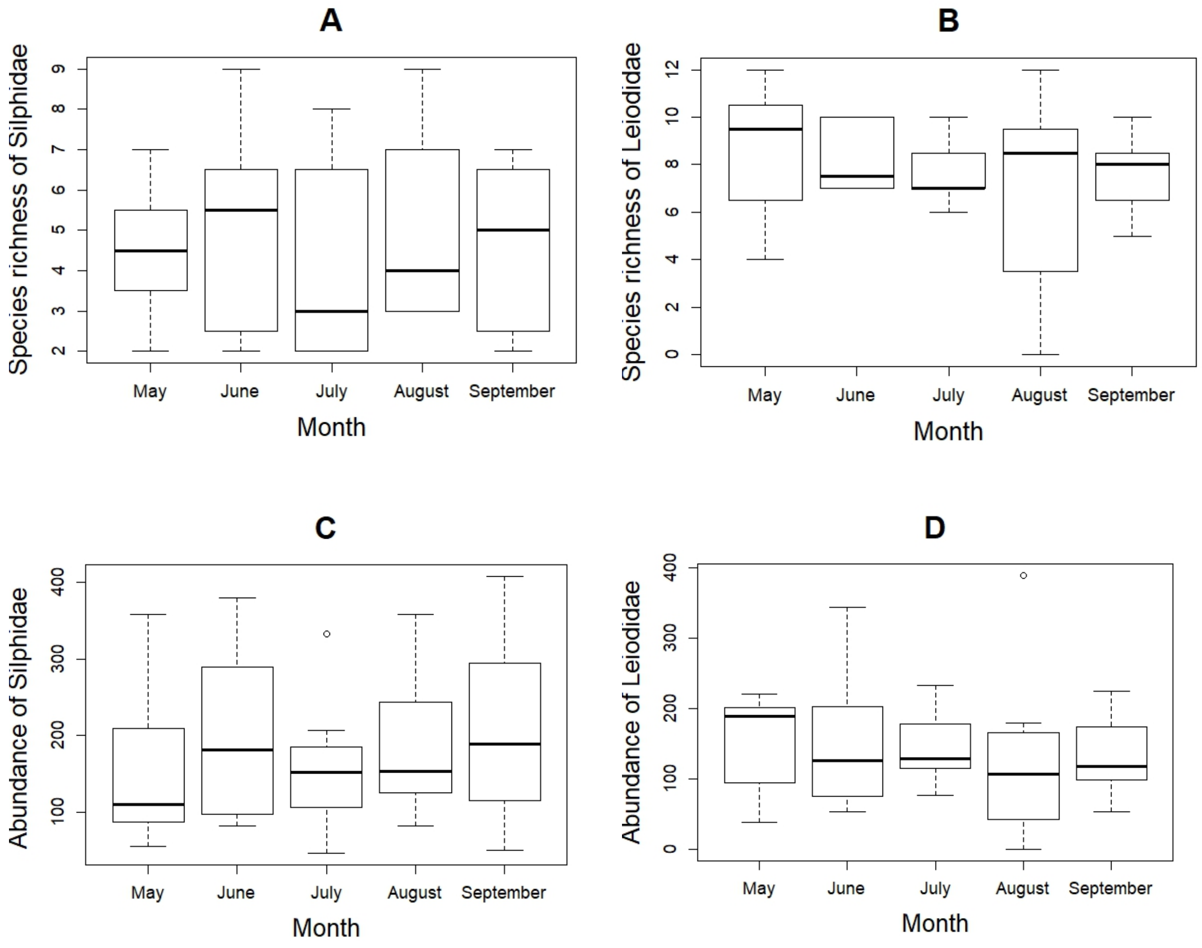
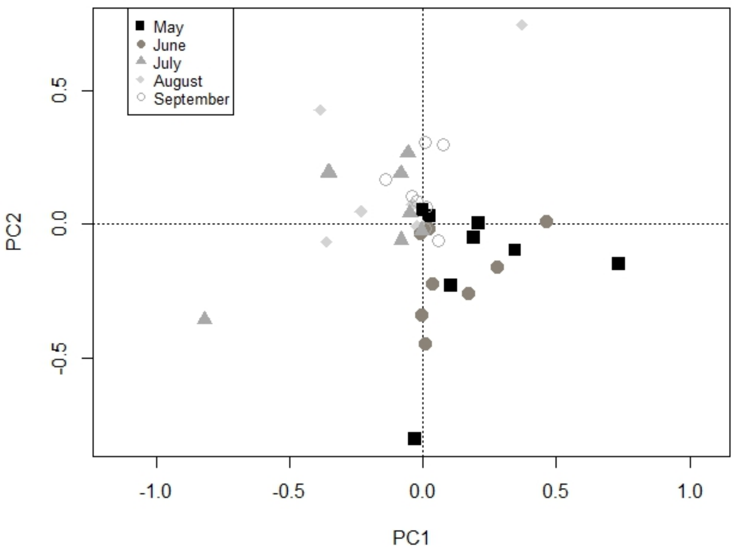


Figure 4 Species richness (a, b) and abundance (c, d) of Silphidae and Leiodidae across the growing season



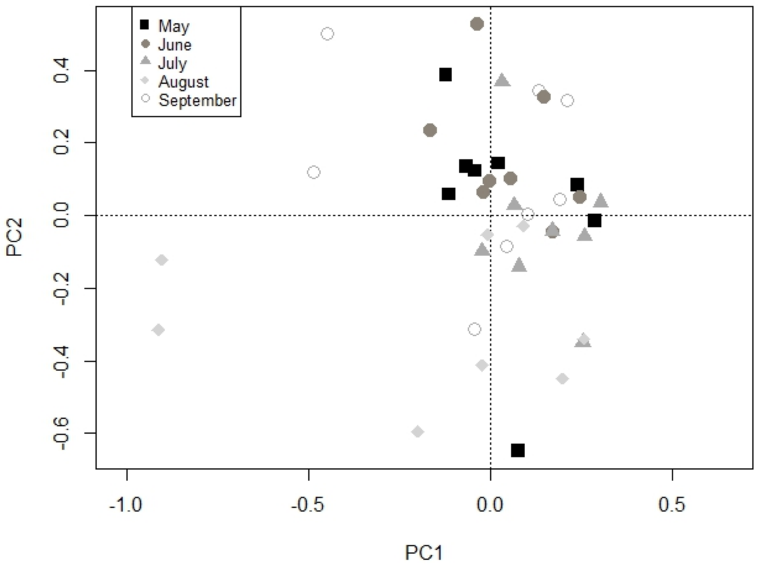


Figure 5 Ordination of Silphidae (a) (PC1=70%, PC2=30%) and Leiodidae: Cholevinae (b) (PC1=8%, PC2=92%) across the growing season

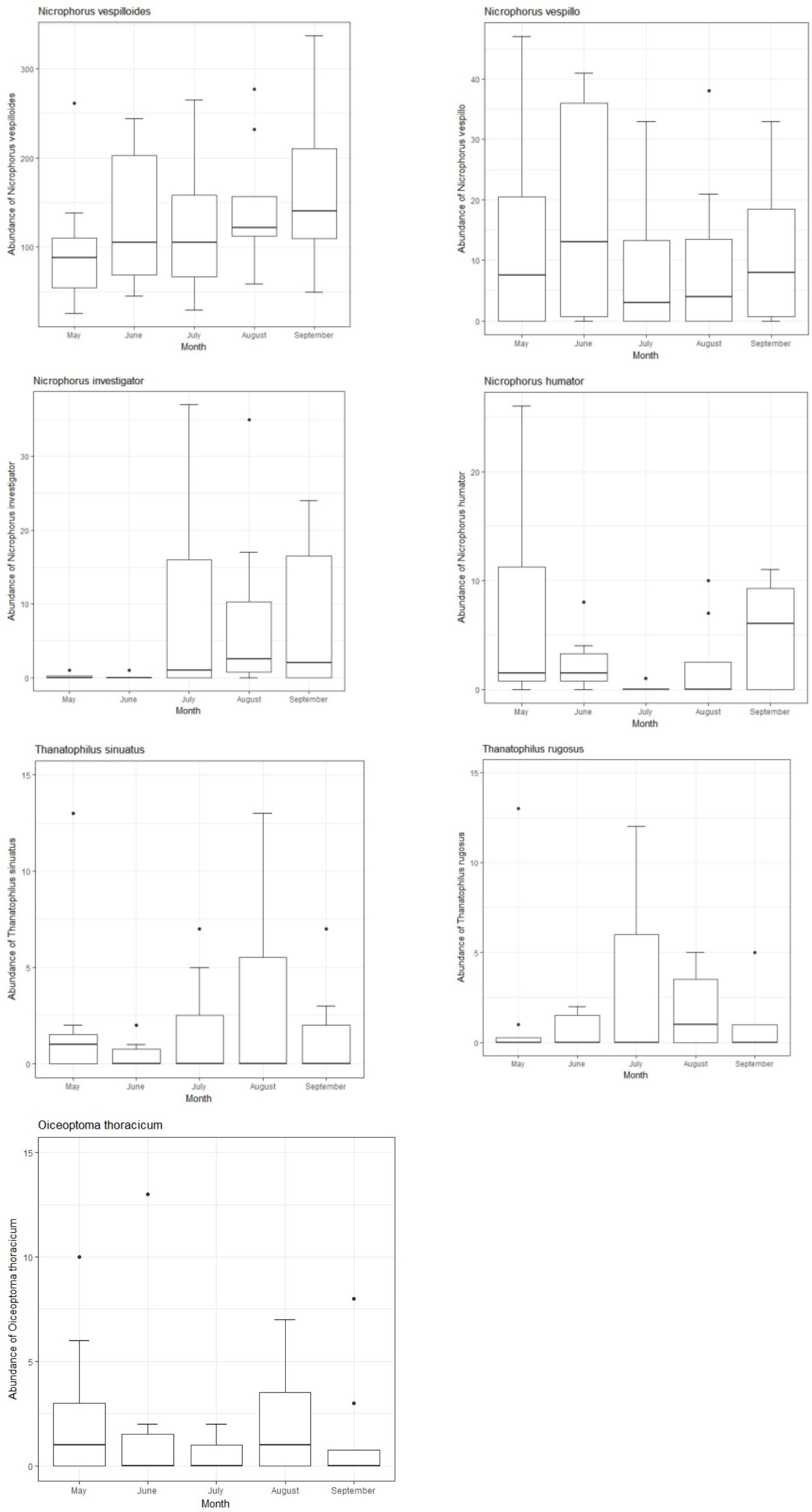


Figure 6 Abundance of the commonest Silphidae species over the growing season: a Nicrophorus vespilloides, b Nicrophorus vespillo, c Nicrophorus investigator, d Nicrophorus humator, e Thanatophilus sinuatus, f Thanatophilus rugosus, g Oiceoptoma thoracicum

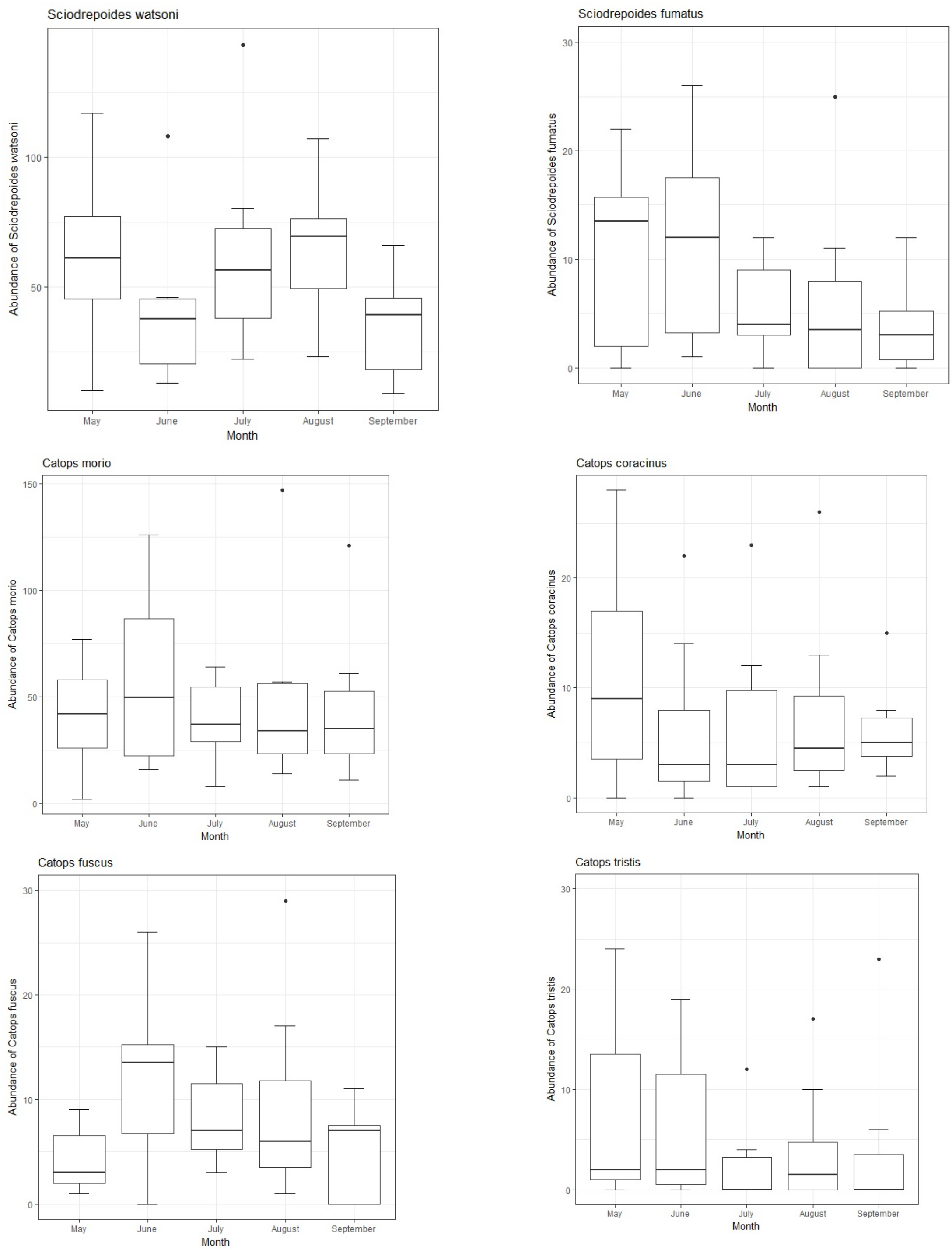


Figure 7 Abundance of the commonest Leiodidae species over the growing season: a Sciodrepoides watsoni, b Sciodrepoides fumatus, c Catops morio, d Catops coracinus, e Catops fuscus, f Catops tristis

Discussion

Overall, the two beetle taxa differed in their response to macrohabitat and growing season. For Silphids, there was a clear distinction of assemblages between forested and unforested habitats and between early and late seasons, despite similar numbers of species and individuals. In contrast, the Cholevids were not as well distinguished by habitat or season, though some specialists of forested macrohabitats were identified, and, fewer species and individuals were found in the unforested macrohabitats overall. These contrasting results highlight the importance of including more than one beetle taxon, with contrasting feeding and behavioural strategies, in studies of carrion beetle ecology.

Macrohabitat associations of carrion beetles

The Silphid beetle assemblages were distinguished between forested and unforested macrohabitats, despite overall similar numbers of species and individuals, indicating that they have a similar capacity to support diverse, but different, communities. Forested and unforested habitats fundamentally differ in ground-level microclimate conditions and soil characteristics (Smith & Heese, 1995; Jakubec & Růžička, 2015). These are important determinants of Silphid habitat preference, linked to their ability to utilise carrion and reproduce in favourable conditions (Jakubec & Růžička, 2015, Wilhelm et al., 2001).

Most (83%) of our collected Silphids were burying beetles in the subfamily, Nicrophorinae. Soil type, depth, consistency and moisture is particularly important for this group, directly affecting their ability to bury carcasses (Wilhelm et al., 2001) and altering the stability of the microclimate (Jakubec & Růžička, 2015). Together, these are key to determining local Nicrophorinae abundance and diversity (Jakubec & Růžička, 2015, Wilhelm et al., 2001, Martín-Vega & Baz, 2012). Indeed, *Nicrophorus vespilloides* constituted 89% of the Silphid catch from the forested sites compared to 52% in unforested sites. This agrees with previous research, indicating that this relatively small species (10-18 mm) prefers the softer, damp soils often in forests for carcass burying (Wilhelm et al., 2001, Scott, 1998, Beninger & Peck 1992). Further, we found *N. vespilloides* dominating in two unforested sites (Grizedale – 98% and Gisburn - 96% of the catch). These were the only two unforested sites with peaty soils, suggesting this soil type represents favourable conditions for this species.

We found *Thanatophilus rugosus, Thanatophilus sinuatus* and *Nicrophorus vespillo* were associated with the unforested macrohabitat, agreeing with previous research (Kočárek, 2001, Dekeirsschieter et al., 2011, Martín-Vega & Baz, 2012). For *Thanatophilus sp.,* Kočárek, 2001 attribute the association with unforested macrohabitats to competition avoidance with *Oiceoptoma thoracicum.* This species similar reproductive behaviours but prefers the forested habitats. However, we sampled O. *thoracicum* but did not find it associated with either macrohabitat. This could be because of one unforested site providing an unusually high 30 specimens compared to the rest of the sites combined total of 3. Unforested habitats have higher ground temperatures in the summer, a possible requirement of larger species to become active (Kočárek, 2001). These conditions may also increase larvae development rates (Wilhem et al., 2001). Indeed, Smith & Heese (1995) suggested that the large species, *N. investigator* (12-22mm) preferred sunny areas due to the warmer soil temperatures. However, whilst we found *N. vespillo* was associated with unforested macrohabitats, *N. investigator*, and another large species, *Nicrophorus humator* (18 -26mm), were not associated with either macrohabitat. This agrees with Scott (1998) who found that *N. investigator* was ubiquitous across forest and field habitats. Further, Kočárek (2001) suggests that *N. investigator*, as one of the few *Nicrophorus* species to be exclusively active during late afternoon and dusk, can avoid competition with other species which are nocturnal or diurnal. This may mean it can inhabit a range of macrohabitats. Further, Smith & Heese (1995) found that another burying beetle, *Nicrophorus defodiens* (Mannerheim, 1846), avoids competition with *N. investigator* by inhabiting shaded macrohabitats. Together, these studies suggest that competitive interactions between species may also play an important role in determining Silphid habitat associations.

Across the unforested macrohabitat sites the Silphid assemblages were more varied than in forests. The unforested macrohabitats had greater variability in local soil conditions, as well as vegetation cover and type, as they ranged from lowland heathland to lowland pasture and upland acid grassland. This variety of heath and grassland, land-uses and site histories may combine to drive differences in assemblage structure. This suggests that the resources and conditions in forested macrohabitats result in a more consistent suite of species, across a large scale and among contrasting forest types (e.g. deciduous woodland and conifer forest), than among unforested grassland and heathland macrohabitats across the same spatial scale. This indicates more research is needed to get a clear understanding of Silphid ecology in a variety of unforested macrohabitats.

In contrast to Silphids, Cholevid assemblages did not differ by macrohabitat type, however, there were significantly more species and numbers of individuals Cholevid in forested compared to unforested macrohabitats. This may be related to a preference for damper soil conditions in forests since previous research found the higher the soil moisture content, the more species of Cholevids (Tizado & Salgado, 2000), although they did note some specialists prefer drier areas. Cholevids are detritivores as well as carrion feeders; in forested habitats there is likely more fungi and decaying organic matter than in unforested habitats (Kočárek, 2002), providing them with a greater diversity in food resources and potentially leading to greater niche availability. Further, we did not find any species associated with unforested macrohabitats, whereas ten (of the total 17) were associated with the forested macrohabitats. Seven of these were from the *Catops* genus, which are known to prefer forested environments (Kočárek, 2002). However, as we found no overall assemblage differences, our study suggested that unforested macrohabitats may provide, in patches, the resources required to support a range of species, but not in the same high numbers as forested areas.

Finally, the deciduous woodlands and conifer plantations were contrasting forest macrohabitats, differing in light availability, forest structure, litter type and ground vegetation as well as site history (e.g. forestry disturbance, longevity of the forest). Despite this, neither Silphids nor Cholevids had different assemblages between the forest types indicating that these parameters are not important determinants of habitat preference for the carrion beetle families we studied. Instead, other factors already discussed, such as soil conditions and availability of carrion or other decaying matter may play a more important role in determining differences between forest types. For instance, Růžička (1994) found *Nicrophorus humator* and *Nicrophorus interruptus* preferred dry and wet coniferous forests respectively. In our study, we sought to control for the influence of soil type and moisture within each site-cluster, in order to minimise these effects, instead seeking to determine the role of macrohabitat parameters. Carrion availability may also be driving differences in Silphid assemblages. For example, the American burying beetle, *Nicrophorus americanus* (Olivier, 1790) prefers areas with high small mammal abundance rather than a specific habitat type (Holloway & Schnell, 1997). Therefore, factors driving distribution of small mammals within and between macrohabitats may be more important for determining assemblage structure than habitat type *per se.*

Seasonal Distribution of carrion beetles

Competition for small mammal carcasses is high; it is a useful but scarce resource that is hard to predict, and so seasonal trends in Silphid activity reflect competition avoidance strategies with other species of Silphids or insect groups (Martín-Vega & Baz, 2012). Indeed, Kočárek, (2001) observed that species of Nicrophorinae have a large fundamental niche in several dimensions and that competition with other carrion invertebrates can restrict that niche. Whilst we found species richness and abundance were similar for both taxa across the growing season, we did find that Silphid assemblages were primarily distinguished between those active in the early growing season (May - June) and those active in later (July – September).

We found *N. investigator* is active from July to September and rarely found in May or June, agreeing with national records (NBN Atlas, 2017). This species overwinters as a pre-pupae and when they have eaten all of the buried carcass, they enter underground chambers and hibernate for up to 11 months before emerging in late June or July the following year (Smith, 2002). We found that *T. rugosus* and *T. sinuatus* are not particularly active in May or June, with *T. rugosus* being prominent in July and *T. sinuatus* being in August. This does not agree with current UK phenological records which show that *T.rugosus* is more active in April and May and *T.sinuatus* being more active in May and June (NBN Atlas, 2017). However, these national records are based from 689 records for *T.rugosus* and 423 for *T.sinuatus*. Our study adds a further 219 and 569 entries respectively, and, suggests that more data is required before the phenology of the less common species is understood. In the UK *T. rugosus* is widespread, whereas *T. sinuatus* more common in the South. However, where these species are found at the same site differences in peak month activity potentially provides a mechanism for niche separation (Kočárek, 2001).

Despite assemblage differences between early and late season and corresponding differences in phenological distribution amongst several species, we found no difference overall in species richness and abundance across the growing season. This is likely due to several common species like *N. vespilloides* and *N. vespillo* being active all growing season. Indeed, this agrees with current records (NBN Atlas, 2017) and may be associated with breeding behaviour. *N. vespilloides* is multivoltine, reproducing up to three times a year (Kočárek, 2001) and can overwinter as both a juvenile and an adult (Meierhofer et al., 1999). Further, we found *N. humator* has a bimodal activity pattern with peaks of activity in May & September. This strategy could be to avoid competition with flies, which have their highest activity in summer (Scott, 1998), June-August in our study. Silphid beetles have been known to abandon a carcass that has been infested with fly larvae (Scott, 1998). In warm weather flies can find a carcass quickly (within 1 hour) and fly infestation can quickly drive the carcass beyond the ideal stage of decomposition for Silphids (Martín-Vega & Baz, 2012; Trumbo, 1990). However, this does not agree with current UK phenological records which show that while *N.humator* is active in May but less so in September, though there is a smaller peak in August (NBN Atlas, 2017). This could be due to recorder effort with a third of records coming from four counties.

In this study, we omitted the March and April collections from this study as no specimens of Silphids were sampled, likely reflecting the colder conditions and lack of carrion resources. In the early season, temperatures are not only colder but also subject to greater fluctuations. At colder temperatures reduced beetle abundance on carcasses has been found (Farwig et al., 2014). Cooler temperatures likely reduce beetle activity but also prevent the beetles from finding the carcass, as less volatiles, that attract them to the carrion, are released (Matuszewski & Szafałowicz, 2013). Further, carrion availability may be lower, due to the lower activity of mammals in winter (Ikeda et al., 2016).

Overall, the Cholevids we sampled did not differ across the growing season by richness, abundance or assemblage structure. This is in contrast with Kočárek, (2002), who was able to distinguish four distinct groups of Cholevids; species active all growing season, species that have a peak of activity in spring, species that have a peak of activity in autumn and species that are bimodal, with peaks of activity in spring and autumn. Despite this, we did find several of the common species conforming to Kočárek's model. *Catops tristis* & *Sciodrepoides fumatus* were found to have a peak of activity in the early growing season. This disagrees with UK phenological records for *Catops tristis,* that has a bimodal distribution and *Sciodrepoides fumatus,* that has a peak of activity in June (NBN Atlas, 2017). However, national records for *Catops tristis* are based on a relatively low number of records – 601, with this study adding a further 371. *Sciodrepoides fumatus* are also based on a relatively low number of records - 236, whereas our study provides a further 671. We also found that these species both favour the forest macrohabitat, and Kočárek, 2002 has suggested that litter cover, which is higher in forests, may mitigate the influence of extremes in temperature. We found *Catops morio* is active throughout the growing season but with a peak in June. This agrees with UK phenological records (NBN Atlas, 2017) in terms of activity throughout the growing season, except for peaking in June. In contrast, we found that *Sciodrepoides watsoni* appears to show peaks of activity in spring (May) and late summer (August). This disagrees with UK phenological records that shows activity throughout the summer (NBN Atlas, 2017). However, whilst these national records are based on a larger number of entries - 781, our study provides a further 2016. There is no species in this study that is highly active in the early autumn (September). This may be due to competition between Silphids and Cholevids for carrion, with the larger Silphids, at this stage of the growing season are feeding, getting ready to overwinter (Kočárek, 2002).

Conclusions

Knowledge of macrohabitat and phenological preferences of insects is important if we are to understand how they might respond to climate and land use change. Yet, to the authors knowledge, this is the first large scale study of the macrohabitat preference and phenology of Silphids & Cholevids in Western Europe. We revealed that Silphid assemblages differ depending on macrohabitat conditions. In the context of carrion insects, their level of habitat specificity coupled with their known response to habitat loss and fragmentation (Martín-Vega & Baz, 2012) makes them possible indicators of changing environments. Cholevid assemblages were not determined by macrohabitat conditions, though common species do exhibit a preference for forested habitats, likely related to soil parameters. However, further investigation is needed to determine the microhabitat factors like soil moisture content, soil temperature and organic matter content which are important for this family (Tizado & Salgado, 2000).

Number of broods per year and how the beetle overwinters may drive phenological trends in Silphid activity over the growing season. Intraspecific competition is also likely be important. For Cholevids this is less clear, several common species were more active earlier in the growing season potentially because of competition with other carrion invertebrates. However, for both groups, exploration of their activity across a full annual cycle will provide useful phenological information, particularly for Cholevids. Indeed, this study has provided a significant number of new records, which in some cases shed new light on our understanding of phenological trends.

Finally, as the first study of British Silphids and Cholevids across multiple geographical locations, time points and macrohabitats we add to the knowledge of their habitat associations and phenology, including for two species of conservation importance - *Nicrophorus interruptus* (Stephens, 1830) and *Catops longulus* (Kellner, 1846) - an important step in their conservation.

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Supplementary material 1 Mouse Baited pitfall trap