HABITAT ASSOCIATIONS OF COEXISTING CARRION BEETLES (SUBFAMILIES NICROPHORINAE AND SILPHINAE) IN SOUTHEASTERN ONTARIO

By

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Abstract

The coexistence of closely related species is thought to play an important role in shaping and maintaining local diversity and community organization. However, competition for shared limiting resources can inhibit coexistence unless species can reduce overlap in resource requirements or minimize differences in competitive ability. Many co-occurring species avoid the costs of coexistence by diverging in habitat use through a process known as habitat partitioning, allowing them to spatially avoid potential competitors. Habitat partitioning appears common among coexisting species and is thought to have important consequences for the evolution of species and traits, and community structure. Yet, despite the commonness of habitat partitioning, little is known about how and when habitat partitioning occurs and its role in facilitating species coexistence. Here, we take the first steps to understanding the role habitat partitioning plays in facilitating coexistence between seven species of burying beetles (genus: *Nicrophorus*) by examining their habitat associations where they co-occur. We test the hypothesis that co-occurring *Nicrophorus* species in southeastern Ontario partition resources by associating with different habitat characteristics or distinct habitat types, potentially to facilitate coexistence. To test this idea, we conducted a large-scale survey of carrion beetle abundance and 54 quantitative habitat characteristics at 100 randomly generated sites spanning an environmentally diverse and heterogenous region of southeastern Ontario. We identified the habitat associations of six co-occurring *Nicrophorus* species and three other carrion beetle species in the subfamily Silphinae. Our findings indicate that co-occurring *Nicrophorus* species do differ in their habitat use in a pattern consistent with habitat partitioning. Specifically, three *Nicrophorus* species (*N. pustulatus, N. hebes*, and *N. marginatus*) were found to be habitat specialists for the forest canopy, wetlands, and open fields, respectively. Three other
Nicrophorus species (N. orbicollis, N. sayi, and N. tomentosus) were found to be habitat generalists with wider breadths of habitat use and high overlap in habitat use with some other species. Our findings suggest that habitat may be an important resource axis along which some Nicrophorus species partition, however, divergence along other resource axes is likely also important for facilitating Nicrophorus coexistence.
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Chapter 1: General Introduction

The Paradox of Species Coexistence

What processes are responsible for the generation and maintenance of the diversity of life? This question lies at the heart of all biology, yet, after centuries of research, universal answers that extend across environments and taxa remain elusive (Lawton 1999; Simberloff 2004; Vellend 2016). Of particular interest to ecologists is understanding how species with similar ecologies and resource requirements coexist within biological communities and how the coexistence of these species influences local diversity (Hutchinson 1959, 1961; Tilman 1982; Chesson 2000). The coexistence of ecologically similar species is paradoxical because traditional ecological theory predicts that competition for shared resources should cause all but one or a few of these species to be excluded from a community (Gause 1932; Hardin 1960; Violle et al. 2011). Contrary to these ideas, however, coexisting ecologically similar species are thought to make up a large component of local diversity and the interactions between them can influence community organization and composition (Toft 1985; Wright 2002; Siepielski and McPeek 2010; Burns and Strauss 2011). Therefore, understanding how and when species coexist is crucial for our understanding of how local diversity is structured and maintained.

Coexistence is especially problematic for closely related species due to their high degree of ecological similarity inherited from a recent common ancestor (Richman and Price 1992; Burns and Strauss 2011). Accordingly, closely related species exhibit high overlap in resource requirements resulting in more intense competition between closely related species than with more distantly related species (MacArthur and Levins 1967; Abrams 1983; Burns and Strauss 2011; Violle et al. 2011). Despite this competition, closely related species from a wide range of taxonomic groups do coexist, including amphibians (Inger and Greenberg 1966; Toft 1980,

Furthermore, the coexistence of closely related species is thought to play an important role in shaping patterns of biodiversity by influencing community structure, the evolution of species traits, and rates of diversification (Brown and Wilson 1956; Richman and Price 1992; Grant and Grant 2006; Price et al. 2014).

Mechanisms of Species Coexistence

Many theories have been proposed to explain how ecologically similar and closely related species achieve coexistence. Notable contributions include the Lotka and Volterra mathematical models of species population dynamics (Volterra 1926; Lotka 1932; MacArthur 1970), community assembly rules (Diamond 1975; Keddy 1992; Weiher et al. 1998), the theory of island biogeography and its subsequent extensions to continental communities (MacArthur and Wilson 1967; MacArthur 1972; Brown and Lomolino 2000), the ecological niche concept and niche theory (Hutchinson 1957; MacArthur and Levins 1967; Vandermeer 1972; Leibold 1995; Holt 2009), the metacommunity concept (Wilson 1992; Zobel 1997; Mouquet and Loreau 2002; Leibold et al. 2004), the neutral theory of species coexistence (Hubbell 2001, 2005; Chave 2004), and modern coexistence theory (Chesson 2000; Adler et al. 2007; HilleRisLambers et al.
Central to many of these theories is the idea that for coexistence to occur, co-occurring species must be able to persist and recover from low abundances when competitor species are at typical abundance levels, thus avoiding local extinction (MacArthur 1972; Chesson 2000). At the local community level, the ability of species to co-occur and meet this requirement is thought to be mediated primarily through species interactions and environmental conditions that act as filters for the kinds of species that can occur within a community (Schoener 1974a, 1983; Schmitt and Holbrook 2003; Burns and Strauss 2011; Violle et al. 2011; HilleRisLambers et al. 2012; Kraft et al. 2015). Modern coexistence theory attempts to provide a comprehensive framework for understanding how co-occurring species coexist at the local community level (Chesson 2000). According to modern coexistence theory, coexistence between species is arbitrated by the interactions between two opposing processes: 1) the evolution of competitive differences between species, and 2) stabilizing mechanisms that reduce species interactions and overlap in resource requirements (Chesson 2000).

Differences between co-occurring species that affect the outcome of competition for limiting resources can act to inhibit coexistence by facilitating competitive exclusion (Gause 1932; Hardin 1960; Violle et al. 2011). Competitively superior species inevitably out-compete competitively inferior species for shared resources, resulting in the exclusion of less competitive species from communities. Differences in competitive ability between species can be reduced, or neutralized, through equalizing mechanisms (Chesson 2000). Equalizing mechanisms such as fundamental trade-offs in traits linked directly to resource acquisition and reproduction, or the density-dependent effects of natural enemies, serve to make co-occurring species competitively equivalent (Chesson 2000; Hubbell 2005; Leibold and McPeek 2006; Adler et al. 2007; Martin 2015). In stable environments, competitively equivalent species will be unable to out-compete
one another for shared resources (Scheffer et al. 2018). Instead, coexistence and the structure of communities would be regulated by stochastic processes that result in random fluctuations in the populations of co-occurring species (Hubbell 2001, 2005; Leibold and McPeek 2006; Vellend 2010). However, there is currently little empirical evidence of species coexistence driven by neutral differences and random processes, nor might equalizing mechanisms alone be enough to completely negate competitive differences between species (Chesson 2000; McGill et al. 2006; Vellend 2010). Furthermore, coexistence may be unlikely to be achieved, even in the absence of competitive differences between species without the additional effects of stabilizing mechanisms (Chesson 2000; HilleRisLambers et al. 2012).

Stabilizing mechanisms are essential for species coexistence and allow co-occurring species to overcome differences in competitive ability by reducing the influence on population growth of interspecific competition relative to intraspecific competition (Chesson 2000; HilleRisLambers et al. 2012). Stabilizing mechanisms function by creating and reinforcing differences in species’ ecologies and resource use, thereby reducing ecological similarity and reliance on shared resources between species. By differentiating in ecology and resource use, competition between species for shared resources is reduced relative to competition within species. Thus, intra-specific competition becomes a greater determinant of the population dynamics of co-occurring species and this can result in frequency-dependent shifts in population growth rates as populations approach their carrying capacity or local extinction (Chesson 2000). When a species is abundant, competition for limited resources increases within species, resulting in a reduction in population growth rates and constraining population size as resource availability declines (Chesson 2000; Adler et al. 2007). In contrast, competition within species decreases when abundance is low, resulting in high resource availability and increased population growth
rates, enabling species to persist and recover when populations near extinction (Chesson 2000; HilleRisLambers et al. 2012). Therefore, stabilizing mechanisms facilitate coexistence by reducing interspecific competition, thus allowing intraspecific competition to constrain population growth and buffer co-occurring species against local extinction (Chesson 2000; Adler et al. 2007; HilleRisLambers et al. 2012).

**Resource Partitioning**

One of the most common and well-studied forms of stabilizing mechanisms is resource partitioning, in which species partition their use of available resources along environmental gradients (Schoener 1968, 1974a, 1986; Ross 1986; Wright 2002). During resource partitioning, co-occurring species diverge in the resources they use or in how they use them, thus reducing overlap in resource requirements and the frequency of competitive interactions (Brown and Wilson 1956; Schoener 1974a; Losos 1994). Species may partition resources along any characteristic of their environment that spans a gradient, however, time, resource type, and space may be particularly important among coexisting species (Schoener 1974a, 1986; Carothers and Jaksić 1984). Species can partition time by diverging in diel or seasonal activity, thus avoiding competitors and potentially gaining access to novel time-sensitive or seasonal resources (Schoener 1974a, 1974b; Ziv et al. 1993; Kronfeld-Schor and Dayan 2003). Species can partition resource types by differentiating in the kinds or sizes of resources they use, for example, by consuming different foods or using distinct nest sites, which can reduce overlap in shared resource requirements (Husar 1976; Ganzhorn 1988; Bootsma et al. 1996; de Mérona and Rankin-de-Mérona 2004). Finally, species can partition spatially by separating their activity along spatially-distributed environmental gradients or between distinct habitat types (Grace and
Regardless of the resources being partitioned, resource partitioning is thought to be an essential process for facilitating species coexistence and shaping species composition, distributions, and abundances within communities (Schoener 1974a, 1986; Toft 1985; Wisheu 1998). Understanding how coexisting species use different resources is essential for understanding how and when such species coexist.

**The Role of Competition in Resource Partitioning**

Despite the importance of resource partitioning for facilitating species coexistence, the mechanisms underlying it remain poorly understood in many systems (Schoener 1982; Connell 1983; Toft 1985; Schluter 2000). Understanding these mechanisms is important in order to identify the conditions where we expect resource partitioning among species, versus the conditions where we expect one species to use all resources to the exclusion of other species. Previously, interspecific competition was often assumed to be the overriding process shaping patterns of resource partitioning. However, some researchers have questioned the role interspecific competition plays in shaping resource partitioning and species coexistence due to the relative lack of explicit testing of interspecific competitions effects on resource use among co-occurring species (Schoener 1983; Niemelä 1993). Fortunately, contemporary studies have since made great progress in furthering our understanding of the mechanisms of resource partitioning, both expanding our knowledge of the role of interspecific competition and extending our knowledge beyond competition to recognize a variety of alternative mechanisms.

Focused investigations into the processes underlying resource partitioning have revealed that while interspecific competition does frequently occur, it is not the only process capable of
producing patterns of differing resource use among co-occurring species (Schoener 1974a; Connell 1983; Wisheu 1998). Predators, parasites, and diseases that do not discriminate between closely related or similar species can increase mortality for all co-occurring species at higher densities, thus favoring divergence in resource use to avoid population clumping (Freeland 1983; Holt and Pickering 1985; Martin 1993, 1996, 1988a, 1988b; Kotler et al. 1991; Begon et al. 1992; Abrams 2000; Feener 2000; Chesson and Kuang 2008; Jachowski et al. 2014). Local adaptation can select for species to specialize and exclusively use resources that optimize competitive and reproductive performance, or to evolve to take advantage of novel resources regardless of interspecific competition (Bouton et al. 1999; Leal and Fleishman 2002; Ellis and Weis 2006; Hereford 2009). Differing dispersal ability between species can differentially limit the local distributions and resources available to co-occurring species (MacArthur 1958; Diamond 1975; Tilman 1997; Chesson and Snyder 2003). Similarly, pre-existing differences in resource use, evolved in areas where species do not co-occur, if conserved, can yield patterns of resource partitioning where they do co-occur in the absence of the effects of interspecific competition (Leibold et al. 2004; Questad and Foster 2008; Lasky et al. 2013; Kraft et al. 2015). Lastly, contemporary patterns of resource partitioning can be the legacy of historical interspecific competition that selected for divergence in resource use in the past but is now no longer relevant (Connell 1980; Pritchard and Schluter 2001). These alternative mechanisms highlight that resource partitioning and coexistence can be more complex than previously thought and that experimental testing is needed to determine how and why co-occurring species differ in resource use.

Interspecific competition is still a pervasive and strongly influential process for shaping patterns of resource use and species coexistence. The occurrence of interspecific competition has
been documented among many coexisting species and evidence from a variety of experimental studies suggests that it often plays a primary role in organizing communities of similar and closely related species (Connell 1961, 1983; Hairston 1980a; Schoener 1983; Robertson and Gaines 1986; Freeman 2015). Field and laboratory experiments that manipulate the co-occurrence and abundances of potential competitors to observe responses in fecundity, survivorship, and population size, have been particularly useful for discerning the role of interspecific competition in producing patterns of resource partitioning (Connell 1961; Schoener 1974a, 1983; Hairston 1980a, 1980b; Heske et al. 1994; Stuart et al. 2014). Such studies have revealed that interspecific competition appears to be responsible for patterns of resource partitioning and species coexistence more often among species that share strongly limiting or homogenously distributed resources, or that experience low levels of predation and parasitism (Connell 1961; Schoener 1983). Additionally, interspecific competition and other mechanisms can act both independently or in combination to produce patterns of resource partitioning and species coexistence (Schoener 1974a, 1983; Connell 1983; Toft 1985; Kotler et al. 1991). Nonetheless, while differences in resource use are commonly described between co-occurring species, interspecific competition cannot simply be assumed to be responsible, nor can patterns of differential resource use be assumed to exist to facilitate coexistence, without explicit testing of the underlying mechanisms.

**Habitat Partitioning**

Many coexisting species avoid the costs of coexistence by evolving to occupy different habitats through a process known as habitat partitioning. Habitat partitioning allows similar and closely related species to coexist by spatially separating potential competitors (MacArthur 1958;
Habitat partitioning may be common among co-occurring taxa around the world and may be an important early step in species divergence and trait evolution (Schoener 1974a; Toft 1985; Richman and Price 1992; Wisheu 1998; Freeman 2015). Likewise, the extent of habitat partitioning among species may be a primary determinant of the number and types of species that can occur in a community (Kadmon and Allouche 2007). Among many co-occurring taxa, habitat partitioning is the most common form of resource partitioning, occurring at significantly greater frequencies and producing larger differences in resource use than either the partitioning of time or resource types (Schoener 1974a, 1986; Toft 1985). The prevalence of habitat partitioning may be due to several factors. Foremost, habitat and spatial gradients are widely available and partitionable. Additionally, unlike time or resource type partitioning, habitat partitioning often does not require complex physiological or morphological adaptations to be facilitated, nor does it incur costs to potential energy or resource gain by limiting the kinds of resources species can use or the time they can spend securing them (Schoener 1974b, 1986). Overall, habitat partitioning appears crucial for facilitating species coexistence, diversification, and community organization.

Despite the apparent ubiquity of habitat partitioning among coexisting species, few general rules have been identified governing how and when habitat partitioning occurs across environments and taxa (Schoener 1974a; Toft 1985). Furthermore, surprisingly little is known about the underlying mechanisms of habitat partitioning or its role in facilitating species coexistence relative to other forms of resource partitioning, such as the partitioning of time or resource types (Wisheu 1998).

Coexisting Carrion Beetles in Southeastern Ontario
In southeastern Ontario, seven species of burying beetle (subfamily: Nicrophorinae, genus: *Nicrophorus*) co-occur despite all requiring a shared, limiting resource for reproduction. These species include *Nicrophorus orbicollis*, *N. sayi*, *N. tomentosus*, *N. pustulatus*, *N. defodiens*, *N. hebes* (previously *N. vespilloides*; Sikes et al. 2016), and *N. marginatus* (Anderson 1982; Anderson and Peck 1985; Beninger and Peck 1992; Robertson 1992). All burying beetle species require the carcasses of small vertebrates for reproduction, which they bury and use as a primary food source and nest for developing larvae (Pukowski 1933; Wilson and Fudge 1984; Anderson and Peck 1985; Scott 1998). However, the availability of small vertebrate carcasses in nature appears limiting and is unpredictable across some levels of time and space (Wilson et al. 1984; Beninger and Peck 1992; Trumbo and Bloch 2002). As a result, co-occurring species of burying beetles face intense competition for suitable carcasses, both within and between species, and with other scavengers (Milne and Milne 1944; Wilson et al. 1984; Otronen 1988; Trumbo 1990). To avoid the costs of coexistence, co-occurring *Nicrophorus* species may have evolved to partition resources along spatial and temporal gradients (Anderson 1982; Wilson et al. 1984; Beninger and Peck 1992). Specifically, evidence suggests that many *Nicrophorus* species have evolved to occupy different habitats. Therefore, investigations into how co-occurring *Nicrophorus* species use habitats differently could further our understanding of the role habitat partitioning plays in facilitating coexistence among closely related species and provide an opportunity to examine potential underlying mechanisms of habitat partitioning.

Previous studies have described the broad habitat associations of *Nicrophorus* species throughout their distributions. *N. orbicollis* has primarily been found in forest habitats; however, they have also been captured in open fields, forest edges, and wetlands (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995; Lomolino et al. 1995; Ratcliffe 1996; Scott
Similarly, *N. sayi* have predominantly been found in forest habitats, especially in coniferous forest, but they have also been captured in open fields at lower abundances (Anderson 1982; Anderson and Peck 1985). In contrast, *N. tomentosus* exhibit a broad pattern of habitat-use and have been found to be abundant in all habitat types (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995; Lomolino et al. 1995; Ratcliffe 1996; Scott 1998; Trumbo and Bloch 2000). Historically, *N. pustulatus* have been an enigmatic species, captured only very rarely in forest habitats and occasionally open fields (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Robertson 1992; Lingafelter 1995; Ratcliffe 1996; Scott 1998). However, compelling evidence suggests that the apparent rarity of *N. pustulatus* may be due to them being specialized to occupy the forest canopy (Ulyshen et al. 2007; LeGros and Beresford 2010; Lowe and Lauff 2012; Dyer and Price 2013; Wettlaufer et al. 2018). *N. defodiens* have been found only in forest habitats, with some evidence indicating that they may prefer dry coniferous forest (Anderson 1982; Anderson and Peck 1985; Trumbo and Bloch 2000). Meanwhile, *N. hebes* have been found almost exclusively in wetland habitats such as Sphagnum bogs and cattail marshes, occasionally occurring in other wetland-bordering habitats (Anderson 1982, Anderson and Peck 1985, Beninger 1989, Beninger 1994, Beninger and Peck 1992, Sikes et al. 2016). Likewise, *N. marginatus* appear to be habitat specialists, only occurring in large open fields and meadows (Anderson 1982; Anderson and Peck 1985; Lingafelter 1995; Lomolino et al. 1995; Ratcliffe 1996; Dyer and Price 2013).

Four other carrion beetle species co-occur with *Nicrophorus* in southeastern Ontario: *Necrophila americana*, *Oiceoptoma inaequale*, *O. noveboracense*, and *Necrodes surinamensis* (subfamily: Silphinae). These species also feed and reproduce on carrion; however, unlike *Nicrophorus*, they do not bury carcasses, do not display complex parental care, and are not
limited to small carcasses for breeding (Anderson and Peck 1985). The general habitat associations of these species have also been previously examined. *N. americana* have been found in forests, open fields, and wetlands, but are often most abundant in forest or wetland habitats (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995; Ratcliffe 1996). *O. inaequale* and *O. noveboracense* have primarily been found in forest habitats, with *O. inaequale* most common in deciduous forest (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995). In addition, both species have also been captured less commonly in open areas and marshes (Anderson 1982). *Necrodes surinamensis* are relatively rare compared to the other carrion beetle species and have typically only been captured in small numbers. They have been found primarily in forest and open field habitats, but have also been captured in wetlands (Ratcliffe 1972; Anderson 1982; Lingafelter 1995; Dyer and Price 2013).

**Scope of this Thesis**

Here, we take the first steps towards understanding the role of habitat partitioning in facilitating the coexistence of *Nicrophorus* species by testing the hypothesis that co-occurring *Nicrophorus* species in southeastern Ontario partition resources by associating with different habitat characteristics or distinct habitat types, potentially to facilitate coexistence. If this hypothesis is true, then we predicted that co-occurring species should be associated with different habitat characteristics within our focal study site (~3,000-hectare reserve). We tested our hypothesis by conducting intensive field surveys of carrion beetle abundance and quantitative habitat characteristics to identify and compare fine-scale differences in habitat associations across *Nicrophorus* species. Our study improves upon previous work by examining the associations between *Nicrophorus* species and 54 local habitat characteristics related to
substrate and vegetative properties within an environmentally diverse and heterogenous region of southeastern Ontario, where seven *Nicrophorus* species and four additional carrion beetle species co-occur. We performed our surveys at random sites encompassing a broad range of potential habitats to accurately reflect the available environmental diversity across the landscape. In addition, we sampled the same sites repeatedly over a four-month period to capture species as they became active throughout the season.
Chapter 2: Methods

Site Description:

We surveyed carrion beetle abundance and measured local habitat characteristics at 100 sites, randomized in their locations (with constraints, detailed below), and spanning the properties of the Queen’s University Biological Station (QUBS), near Elgin, Ontario, Canada (Fig. 1A & 1B). These sites have been previously used for a variety of long-term studies and were originally selected by randomly generating GPS coordinates that fell within the QUBS property boundaries. We restricted initial random coordinates by two criteria: 1) sites needed to be at least 400m apart, and 2) sites could not fall in open water. The resultant sites span an area over 2690 hectares in size encompassing a broad variety of habitats including deciduous and mixed hardwood forests, conifer plantations, pine-studded rock outcrops, white cedar bogs, cattail marshes, swamps, small lakes and beaver ponds, and reclaimed agricultural fields.

Survey of Carrion Beetle Abundance:

We surveyed carrion beetle abundance between April and October 2017 using lethal pitfall traps set for seven days at a time (Wettlaufer et al. 2018). At each site, we simultaneously set one ground-level trap and a second canopy-level trap hung 6m above from a nearby tree branch. Our traps consisted of yellow plastic buckets 35cm deep and 17cm wide filled with approximately six inches of saturated saline water and baited with frozen chicken wings wrapped in cheesecloth. We suspended the chicken wings above the saline solution by wrapping a piece of steel craft wire around the chicken and attaching it to the center of a 35cm² square of chicken wire placed over the opening of the bucket. To prevent rainfall from entering the bucket, we
covered each trap with a 30cm² plywood board elevated slightly above the bucket’s lip. We then placed large stones on top of the board to deter vertebrate scavengers from disturbing the traps. We set traps at each site three to four times over the course of the sampling period and collected all carrion beetles belonging to the family Silphidae. We then identified all carrion beetles to species and sexed them following Anderson and Peck (1985).

**Fig 1.** (A) Map of the 100 randomly generated sampling sites where we conducted our surveys of carrion beetle abundance and local habitat characteristics on the main properties of the Queen’s University Biological Station (QUBS). All sites are at least 400m apart and do not fall within bodies of water. (B) Sampling sites located on the Bracken tract properties of QUBS. Sites are color-coded based on the six general habitat categories assigned during our survey of habitat. The boundaries of the QUBS properties are marked by orange border lines. Base map from Google Maps (Google 2019).
Survey of Local Habitat Characteristics:

To examine the habitat associations of the collected carrion beetle species, we conducted surveys of local habitat characteristics at each of our 100 sites following a modified version of the Breeding Biology Research and Monitoring Database (BBird) field protocol for measuring vegetation (Martin et al. 1997). While originally designed for describing bird nesting sites, the BBird protocols provide comprehensive standardized methods for measuring quantitative ground cover and vegetation characteristics that may also be relevant to burying beetles.

Ground Cover, Leaf Litter, and Soil Characteristics:

To examine the properties of the ground cover, leaf litter, and soil, we established a circular 2.5m radius plot centred on the ground-level trap at each site. We measured 2.5m from the ground-level trap in the four cardinal directions and marked these points with trail flagging tape to signify the edges of the plot. From outside of the plot, we categorized ground cover into thirteen categories and estimated the relative percentage of plot area covered by each (Table S1). To measure leaf litter depth, we dug a small 20cm deep hole and used a ruler to measure from the top of the surface leaf litter to the soil depth at which large leaf particulate was no longer observed in the soil. We measured soil depth by pushing a 1.5m metal rod into the soil until unyielding resistance was met and measuring the length that the pole had extended below ground. We measured soil depth at four different locations in each quadrant of the plot and once at the center. We then averaged the five measures to calculate average soil depth for the site and noted the dominant soil (i.e. most common) type observed.
Habitat Type, Tree Species Diversity, and Tree Size:

To examine the number and types of trees at each site, we established a circular 17.25m radius plot centred on each ground-level trap. We measured 17.25m from the ground-level trap in the four cardinal directions and marked these spots as the edges of the plot with trail flagging tape. Within this plot, we measured the diameter at breast height (DBH) and identified to species every tree with a DBH greater than 9cm. We then categorized the forest canopy as open or closed based on whether there was dense tree cover above the site. We also placed each site into one of six general habitat categories based on the dominant vegetation and substrate type (Table S1). Finally, using the data on tree species abundance and size, we generated an additional five variables for each site: the total number of tree species identified, the total number of trees counted, and the number of small (9 to 23cm DBH), medium (23 to 38cm DBH), and large (>38cm DBH) trees counted within the plot.

Statistical Analyses:

In total, we caught 13,153 carrion beetles in 604 successful trapping events with all seven Nicrophorus and four Silphinae species represented (Table 1). Prior to analyses, we removed any traps that were disturbed by vertebrate scavengers from the dataset. For our statistical analyses, we calculated the mean abundance of each carrion beetle species in the ground and canopy traps for each site over the entire trapping period. We used these values as our measure of carrion beetle abundance at each site, with ground and canopy traps handled separately.
Table 1. Counts of carrion beetles collected in ground- and canopy-level traps between April and October 2017 during our survey of carrion beetle species abundance on the properties of the Queen’s University Biological Station.

<table>
<thead>
<tr>
<th>Nicrophorinae Species</th>
<th>Ground-Level</th>
<th>Canopy-Level</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of Individuals</td>
<td>Number of Traps</td>
<td>Number of Individuals</td>
</tr>
<tr>
<td><em>N. orbicollis</em></td>
<td>3565</td>
<td>180</td>
<td>875</td>
</tr>
<tr>
<td><em>N. sayi</em></td>
<td>629</td>
<td>138</td>
<td>268</td>
</tr>
<tr>
<td><em>N. tomentosus</em></td>
<td>1714</td>
<td>99</td>
<td>1905</td>
</tr>
<tr>
<td><em>N. pustulatus</em></td>
<td>37</td>
<td>16</td>
<td>491</td>
</tr>
<tr>
<td><em>N. defodiens</em></td>
<td>10</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td><em>N. hebes</em></td>
<td>83</td>
<td>21</td>
<td>22</td>
</tr>
<tr>
<td><em>N. marginatus</em></td>
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<table>
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<th>Silphinae Species</th>
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<th>Canopy-Level</th>
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<td></td>
<td>Number of Individuals</td>
<td>Number of Traps</td>
<td>Number of Individuals</td>
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<td>156</td>
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<tr>
<td><em>O. inaequale</em></td>
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<td>79</td>
<td>12</td>
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<tr>
<td><em>O. noveboracense</em></td>
<td>119</td>
<td>50</td>
<td>12</td>
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<tr>
<td><em>N. surinamensis</em></td>
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<td>11</td>
<td>17</td>
</tr>
<tr>
<td>Total</td>
<td>9391</td>
<td>277</td>
<td>3762</td>
</tr>
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</table>

*Conditional Inference Tree Classification:*

All statistical analyses were performed in R version 3.5.1 (R Core Team 2018). To examine the associations between the mean abundances of carrion beetle species in traps, averaged across all trapping events at each site, and the local habitat characteristics surveyed, we generated conditional inference trees using the function “ctree” from the R-package “partykit” version 1.2-2 (Zeileis and Hothorn 2012). Conditional inference trees are a form of decision tree that use regression model estimates and binary recursive partitioning to group and classify data using a set of predictor variables (Hothorn et al. 2006). First, ctree estimates a regression relationship between the response variable and each predictor variable using binary recursive partitioning within a conditional inference framework. At each node of the tree, the null
hypothesis of independence between each predictor variable and the response variable is tested individually, and a significance value (p) assigned. The predictor variable with the lowest significance value is then used to split the data, provided that value falls below a threshold of 0.05. Splitting continues at each node down the tree until no predictor variables are found to be significantly associated with the response variable, at which point splitting stops. In our conditional inference trees, mean abundance of each species in ground and canopy traps at each site was used as the response variable while trap type (ground or canopy) and all 54 measured habitat characteristics were used as the predictor variables. Including all 55 variables allowed us to identify and describe the relationships between the habitat characteristics that most strongly influenced the abundance of each carrion beetle species within each trap. Additionally, we repeated our conditional inference tree analyses for each carrion beetle species using occurrence instead of mean abundance as the response variable. We converted our abundance data into occurrence data by recoding all mean abundances greater than zero as “present” and all zero values as “absent”. This allowed us to identify the habitat characteristics that best predicted whether a species was present or absent within a trap.
Chapter 3: Results

Habitat Associations of Carrion Beetle Species:

Our conditional inference tree analyses identified significant associations between the local habitat characteristics that we measured and the abundances and occurrence (presence versus absence) of eight carrion beetle species. *N. orbicollis* abundance was greater in ground-level traps (n = 100 traps; Fig. 2A) and *N. orbicollis* were present in more traps at sites with many trees (n = 188 traps; Fig. 2B). *N. sayi* abundance was also greater in ground-level traps. However within ground-level traps, *N. sayi* abundance was higher at sites with deeper leaf litter (n = 16 traps) and a greater number of red oak (n = 13 traps), sugar maple (n = 18 traps), white pine (n = 7 traps), and small trees (n = 14 traps; Fig. 3A). *N. sayi* were present in a greater number of traps at sites with high numbers of trees (n = 188 traps; Fig. 3B). *N. tomentosus* exhibited no significant associations with any of the habitat characteristics that we measured. They were abundant (n = 199 traps; Fig. 2C) and present (n = 199 traps, Fig. 2D) in most traps that we surveyed. Both *N. pustulatus* abundance (n = 100 traps; Fig. 4A) and presence (n = 100 traps; Fig. 4B) were greater in forest canopy-level traps. In contrast, no significant associations were found between *N. defodiens* abundance or occurrence and the habitat characteristics that we measured. *N. defodiens* was found in low abundance when they were captured and were absent from most traps (n = 199 traps; Fig. 5A & 5B). *N. hebes* abundance was greater in traps located within wetlands (n = 9 traps; Fig. 4C). However, *N. hebes* presence was not associated with any specific habitat characteristics. Instead, *N. hebes* were found to be absent from most traps (n = 199 traps; Fig. 4D). Both *N. marginatus* abundance (n = 8 traps; Fig. 4E) and presence (n = 8 traps; Fig. 4F) were greater in traps located within open fields. *Necrophila americana* abundance (n = 100 traps; Fig. 6A) and presence (n = 100 traps; Fig. 6B) were greater in ground-level traps.
*O. inaequale* abundance was greater in ground-level traps (n = 100 traps; Fig. 6C). *O. inaequale* were most often present in ground-level traps, (n = 100 traps) but were also present in some canopy-level traps at sites with many red oak trees (n = 15 traps; Fig. 6D). *O. noveboracense* abundance (n = 100 traps; Fig. 6E) and occurrence (n = 100 traps; Fig. 6F) were greater in ground-level traps. Lastly, *Necrodes surinamensis* abundance and occurrence was not associated with any habitat characteristics. They were found in low abundance overall and were absent from most traps (n = 199 traps; Fig. 5C & 5D).

**Fig 2.** Conditional inference trees showing significant associations between local habitat characteristics and (A) *N. orbicollis* mean abundance, (B) *N. orbicollis* occurrence, (C) *N. tomentosus* mean abundance, and (D) *N. tomentosus* occurrence. Boxplots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. n-values indicate the number of traps (ground and canopy) included in each node. *N.*
orbicollis abundance was greater in ground-level traps and they were present (dark shading) in a greater number of traps at sites with many trees. Neither N. tomentosus abundance nor occurrence were not significantly associated with any local habitat characteristic.

![Figure 3](image-url)

**Fig 3.** Conditional inference trees displaying significant associations between (A) *Nicrophorus sayi* mean abundance and (B) *N. sayi* occurrence and local habitat characteristics. Boxplots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. n-values indicate the number of traps (ground and canopy) included in each node. *N. sayi* abundance was greater in ground-level traps at sites with deep leaf litter and
many red oak, sugar maple, white pine, and small trees. *N. sayi* were present (dark shading) in a greater number of traps at sites with many trees.

![Conditional inference trees](image)

**Fig 4.** Conditional inference trees displaying significant associations between local habitat characteristics and (A) *N. pustulatus* mean abundance, (B) *N. pustulatus* occurrence, (C) *N. hebes* mean abundance, (D) *N. hebes* occurrence, (E) *N. marginatus* mean abundance, and (F) *N.
marginatus occurrence. Boxplots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. n-values indicate the number of traps (ground and canopy) included in each node. Both N. pustulatus abundance and presence (dark shading) were significantly greater in canopy-level traps. N. hebes abundance was greater in traps located in wetland habitats, while N. hebes occurrence was not significantly associated with any habitat characteristics. N. marginatus abundance and presence (dark shading) were greater in traps located in open field habitat.

![Diagram of abundance and occurrence](image_url)

**Fig 5.** Conditional inference trees displaying significant associations between local habitat characteristics and (A) *N. defodiens* mean abundance, (B) *N. defodiens* occurrence, (C) *Necrodes surinamensis* mean abundance, and (D) *Necrodes surinamensis* occurrence. Boxplots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. n-values indicate the number of traps (ground and canopy) included in each node. No significant associations were identified between any habitat variables and the mean abundance or occurrences of either species.
Fig 6. Conditional inference trees displaying significant associations between local habitat characteristics and the abundances and occurrence of three Silphinae species. Boxplots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. n-values indicate the number of traps (ground and canopy) included in each node. (A) Necrophila americana mean abundance and (B) occurrence were greater in ground-level traps. (C) Oiceoptoma inaequale mean abundance was greater in ground-level traps. (D) O. inaequale were present (dark-shading) in a greater number of ground-level traps,
but they were also present in some traps at canopy-level at sites with many red oaks. \( \text{E} \) O. noveboracense mean abundance and \( \text{F} \) occurrence were greater in ground-level traps.
Chapter 4: Discussion

Co-occurring species of carrion beetles may partition resources to avoid interspecific competition and achieve stable coexistence. Here, we tested the hypothesis that co-occurring Nicrophorus species in southeastern Ontario partition resources by associating with different habitat characteristics or distinct habitat types, thus potentially facilitating coexistence. We predicted that if co-occurring species partition habitat, then they should be associated with different habitat characteristics within our focal study site. Using survey data on carrion beetle abundance, occurrence, and quantitative local habitat characteristics collected from sampling sites across a environmentally diverse study site in southeastern Ontario, we successfully identified the habitat associations of six carrion beetle species in the subfamily Nicrophorinae (Nicrophorus) and three species in the subfamily Silphinae (Necrophila, Oiceoptoma, Necrodes). Co-occurring Nicrophorus species were found to differ in habitat use in a pattern consistent with habitat partitioning, supporting our hypothesis. The patterns of habitat-use revealed in this study suggest that the carrion beetle assemblage in southeastern Ontario consists of a mixture of habitat generalists, capable of living in a variety of conditions, and specialists that restrict their activity to specific habitats (Fig. 7).

Habitat Associations of Nicrophorinae

Our conditional inference trees predicting N. orbicollis abundance and occurrence showed that the species occupies a range of different environments, but occurs, and is most abundant in, dense forest habitats. N. orbicollis were abundant in most ground-level traps and occurred at more sites with many trees (Fig. 2A & 2B). These results suggest that N. orbicollis
occur in almost all the environments we sampled, regardless of local habitat characteristics, but are less abundant in the forest canopy and are more likely to occupy forested areas. Forests may represent high quality habitat for *N. orbicollis*. Soils in temperate forests, such as those found at our study site in southeastern Ontario, may possess properties that make them ideal for carcass burial. In choice experiments, *N. orbicollis* prefer to bury carrion in soils with high organic content, such as leaf litter, as it can provide increased structural support to their brooding chambers (Muths 1991). Likewise, *N. orbicollis* may prefer very moist alluvial and sandy loam soils in temperate forests, such as those found at our study site in southeastern Ontario, may possess properties that make them ideal for carcass burial.
soils, soil types that are common in temperate forests (Bishop et al. 2002; Willemssens 2015). The temperature in forests may also provide an ideal range for *N. orbicollis*. Temperature can play an important role in influencing burial times (Scott 1990), the outcome of competition (Wilson et al. 1984; Merrick and Smith 2004), rates of larval development (Smith and Heese 1995; Meierhofer et al. 1999; Nisimura et al. 2002), and activities such as flight among *Nicrophorus* species (Merrick and Smith 2004). Forest canopy can have a moderating effect on below-canopy air temperature and humidity, causing maximum temperatures to be lower, and minimum temperatures and air humidity to be higher, as well as blocking UV radiation (Grimmond et al. 2000; Renaud et al. 2011; Von Arx et al. 2012). The temperature and humidity effects are particularly important at night when *N. orbicollis* are active since forest canopy can buffer nocturnal heat and air moisture loss to maintain higher air temperatures and relative humidities (Renaud et al. 2011; Von Arx et al. 2012). Large beetles like *N. orbicollis* are prone to over-heating during intense activities such as flight, but can also struggle to produce enough energy for activity at cooler temperatures (Merrick and Smith 2004). The buffering effect of forest canopy may prevent temperatures from rising to lethal limits for *N. orbicollis* while keeping temperatures above the minimum required for activity. Therefore, *N. orbicollis* may be able to be active on a greater number of nights within forests compared to in other habitats.

*N. sayi* appear to be primarily associated with dense forest habitats at ground-level. Specifically, *N. sayi* were more abundant at sites with deep leaf litter and many red oaks, sugar maples, white pine, and other small trees, and were present at sites with many trees (Fig. 3A & 3B). Despite occupying similar forest habitat as other *Nicrophorus* species, *N. sayi* emerge earlier in the spring and experience different environmental conditions as a result (Anderson 1982; Anderson and Peck 1985; Wettlaufer 2019). Spring conditions in temperate regions like
southeastern Ontario are typically colder and wetter than at other times of the year, and small vertebrates are rarer due to winter mortality (Environment Canada Climate Normals 1981 to 2010; Pucek et al. 1993). Often open habitats and those with shallow soil-layers become flooded with snow-melt and rain, likely becoming unusable to burying beetles active at the time (Cavallaro et al. 2017). Forests with deep leaf litter layers may provide one of the few places where soils remain suitable for carcass burial and deep leaf litter may allow beetles to dig structurally stable burrows that more effectively insulate the brooding chamber (Muths 1991; Parajulee et al. 1997; Trumbo and Bloch 2002). In addition, the tree species that *N. sayi* are associated with produce seeds consumed by many small vertebrates. These types of trees provide a vital source of food and refuge for overwintering and emerging small mammals; therefore, these animals tend to concentrate their activity around them (Miller and Getz 1977; Dueser and Shugart 1978; Pyare et al. 1993; Schnurr et al. 2004). The areas around these trees may act as hotspots of small vertebrate activity and increased small vertebrate carrion availability, which could explain why *N. sayi* are found in greater abundance nearby.

*N. tomentosus* have the broadest pattern of habitat use among the *Nicrophorus* species of southeastern Ontario. They occurred abundantly across all environments and both abundance and occurrence were not associated with any specific habitat characteristics (Fig. 2C & 2D). These patterns suggest that *N. tomentosus* are habitat generalists, possessing broad environmental tolerances that allow them to survive and reproduce in a wide variety of habitats with vastly different conditions (McPeek 1996; Bonier et al. 2007). Despite overlapping in habitat-use with congeners, *N. tomentosus* can occupy the same habitats and avoid competition by becoming reproductively active after the reproductive season of many of the other carrion beetle species has ended (Anderson 1982; Wilson et al. 1984; Wettlaufer 2019). *N. tomentosus* begin emerging
in early August and remain active until late October (Anderson 1982; Anderson and Peck 1985; Wettlaufer 2019). During this time period, environmental conditions in southeastern Ontario undergo rapid and dramatic changes in temperature, rainfall, and day-length (Environment Canada Climate Normals 1981 to 2010). As such, *N. tomentosus* could require broad environmental tolerances to cope with the changing climatic conditions. Part of this tolerance may be facilitated through behavioural traits. *N. tomentosus* are active diurnally and submerge carcasses in shallow pits under groundcover rather than fully burying them (Shubeck 1971; Anderson and Peck 1985). By shifting their activity to earlier in the day and reducing the time required to prepare carrion by burying carcasses in shallow pits, *N. tomentosus* may be able to find and secure carcasses quickly while temperatures are higher during the day. Furthermore, burying carrion in shallow pits under groundcover may reduce the influence of local soil properties on brood chamber structure and larval development, while also aiding in reducing flood risk. In addition, the larvae of *N. tomentosus* may be particularly tolerant of challenging conditions, as the species uniquely overwinters in the larval stage and face the environmental extremes of winter as larvae (Anderson 1982). *N. tomentosus* may possess traits that confer broad tolerance to seasonally changing environmental conditions and this may also allow them to take advantage of many different habitats.

*N. pustulatus* have historically been regarded as an enigmatic species rarely captured in field surveys and little is known of their natural history (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Robertson 1992; Lingafelter 1995; Ratcliffe 1996; Scott 1998). Recent evidence suggests that their apparent rarity may be due to them being forest canopy specialists and therefore less likely to be captured in the ground-level pitfall traps typically employed (Ulyshen et al. 2007; LeGros and Beresford 2010; Lowe and Lauff 2012; Dyer and Price 2013;
Our results provide further evidence supporting the idea that *N. pustulatus* are forest canopy specialists. In our analyses, high *N. pustulatus* abundance and occurrence were best predicted by forest-canopy level traps (Fig. 4A & 4B); no other habitat variables predicted *N. pustulatus* occurrence or abundance. By diverging into the forest canopy, *N. pustulatus* may be able to escape competition with co-occurring congeners and take advantage of novel canopy resources (Ulyshen et al. 2007; Wettlaufer et al. 2018). Other carrion beetle species are largely absent from the forest canopy or occur in substantially lower abundances (Ulyshen et al. 2007; Dyer and Price 2013; Wettlaufer et al. 2018). These species may be unable to meet the energetic demands and lack the maneuverability required to maintain flight to search for carrion in the forest canopy (Berwaerts et al. 2002; Merrick and Smith 2004; Wettlaufer et al. 2018). Meanwhile, many small vertebrates like birds use tree cavities and branches located in the upper forest canopy as nesting sites during their breeding season, providing a reliable source of carrion for *N. pustulatus* (Ricklefs 1969). *N. pustulatus* are also capable of reproducing on larger carcasses (>100g) and can produce significantly more offspring than congeners, which could allow them to maximize reproductive output when opportunities present themselves if carrion is rare in the canopy (Robertson 1992; Trumbo 1992). However, how *N. pustulatus* bury carrion in the forest canopy is currently not well understood. *N. pustulatus* have been demonstrated to bury carcasses like other *Nicrophorus* species when provided suitable substrate in laboratory experiments (Robertson 1992), and have been observed to bury nestling bird carcasses in nest lining within a nest box of Tree Swallows (*Tachycineta bicolor*; Wettlaufer et al. 2018). To date, *N. pustulatus* reproduction in the forest canopy has not been observed in nature and the natural history of the species remains enigmatic.
Neither *N. defodiens* abundance nor occurrence were associated with any of the habitat characteristics we surveyed. *N. defodiens* were predicted to be either rare or absent in most traps, regardless of the surrounding environment, suggesting that this species is rare at our study site (Fig. 5A & 5B). In total, only 14 individuals were captured at 10 different sites over our entire sampling period (Table 1). Previous studies have reported strong associations between *N. defodiens* and forested habitats and indicate they may prefer dry coniferous forest (Anderson 1982; Anderson and Peck 1985; Trumbo and Bloch 2000). Our analyses may have been unable to identify any significant associations between *N. defodiens* and local habitat characteristics due to the low number of *N. defodiens* captured in our survey, and the rarity of coniferous forest at our study site (only two of our trapping sites were located within coniferous forest; Fig. 1A). Alternatively, *N. defodiens* could be generally rare in southeastern Ontario. Other surveys of carrion beetle abundance in southeastern Ontario performed by Anderson (1982) and Robertson (1992) also found *N. defodiens* to be uncommon in the region.

The habitat associations of *N. hebes* indicate that they are wetland specialists, as has previously been suggested (Anderson 1982; Beninger and Peck 1992; Sikes et al. 2016). Our analysis found that *N. hebes* abundance was greater in wetland habitats than in all other habitat types combined. *N. hebes* occurrence was not associated with any habitat characteristics (Fig. 4C & 4D), likely reflecting our ability to trap *N. hebes* in small numbers in other habitats, provided that wetlands are nearby. The presence of open water, water-saturated and oxygen-limited soils and acidic or basic pH-levels common in wetlands likely pose substantial challenges for burying beetles (Batzner and Wissinger 1996), leading to the question of how *N. hebes* is able to breed in wetland habitat. In captivity, *N. hebes* have been demonstrated to bury carcasses and rear broods like other *Nicrophorus* species when provided suitable soil, suggesting they do not exhibit an
alternative reproductive strategy (Beninger 1989). *N. hebes* instead likely possess unique adaptations that aid in survival and reproduction in wetland environments, and they may restrict their activity to areas within wetlands that facilitate carcass burial. Burying beetles have been shown to tolerate immersion under water and hypoxic conditions better than non-burying carrion beetles, but performance differs between *Nicrophorus* species, and *N. hebes* has not been specifically tested (Cavallaro et al. 2017). In any case, adult *N. hebes* can likely escape submersion by avoiding pools of open water and retreating above ground when water levels rise. Burial chambers in wetlands, however, likely become inundated with water frequently, and thus *N. hebes* larvae may require adaptations to frequent immersion and hypoxia. For example, the larvae of marsh-dwelling tiger beetles (spp. *Cicindela togata*) can survive up to 6 days submerged underwater by severely reducing metabolic activity via dormancy and using anaerobic metabolic pathways (Hoback et al. 1998; Hoback and Stanley 2001). Alternatively, some terrestrial insects frequently exposed to submersion can trap small air bubbles on their bodies to serve as a physical gill or absorb oxygen from water directly through their cuticle (Foster and Treherne 1976; Hoback and Stanley 2001; Pedersen and Colmer 2012). In addition, flooding in *Nicrophorus* burial chambers can result in the release of volatile organic compounds from buried carcasses and the presence of these compounds can interfere with the beetle’s metabolic pathways and reduce the time beetles can survive immersed (Cavallaro et al. 2017). In response, *N. hebes* may bury carcasses close to the surface in shallow pits like their sister species *N. vespilloides* or, when possible, hide carcasses under groundcover to prevent complete restriction of airflow (Pukowski 1933; Anderson and Peck 1985). Furthermore, to limit the risk of submersion, *N. hebes* may limit their activity to areas within wetlands with drier substrate
such as sphagnum moss, shorelines, and raised islands (Beninger 1989, 1994; Beninger and Peck 1992).

*N. marginatus* were also identified as habitat specialists and were significantly more likely to occur, and be abundant, in open fields than in other habitats (Fig. 4E & 4F). These findings are consistent with the conclusions of most existing literature on *N. marginatus* habitat associations (Anderson 1982; Anderson and Peck 1985; Lingafelter 1995; Lomolino et al. 1995; Ratcliffe 1996; Dyer and Price 2013). However, very few *N. marginatus* were captured in our survey. Over the entire survey, only 3 individuals were collected from a single trap (Table 1). This contrasts with other parts of their range where *N. marginatus* are among the most abundant *Nicrophorus* species (Lingafelter 1995; Backlund and Marrone 1997). *N. marginatus* has been suggested to prefer very large open fields and meadows greater than 25 hectares in size (Trumbo and Bloch 2000). This preference may have limited our ability to capture the species, as large fields are uncommon in our study area and we successfully trapped *N. marginatus* at only one open field site. Regardless, open fields likely present considerable challenges for *Nicrophorus* species. Lacking any forest canopy, open fields are exposed to high levels of sunlight and rainfall. As a result, the ambient air and soil conditions in open fields during the summer are often hotter, drier, and prone to temporary flooding (Renaud et al. 2011; Von Arx et al. 2012). Interestingly, *N. marginatus* have been found to exhibit relatively high rates of water loss in dry, low humidity conditions, contrary to what would be expected based on their habitat associations (Bedick et al. 2006). To avoid desiccation and lethal temperatures, they may respond to dry conditions by limiting their activity to times of the day when temperatures are cooler and spending their time burrowed in moist soils within fields (Bedick et al. 2006). Currently, little is
known of what other adaptations *N. marginatus* may possess for circumventing the challenges presented by open field conditions.

**Habitat Associations of Silphinae**

The four Silphinae carrion beetle species included in our analyses were all found to display generalist habitat preferences consistent with existing literature (Ratcliffe 1972, 1996; Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995; Dyer and Price 2013). *Necrophila americana* were found to be abundant and present in ground-level traps in all habitat types (Fig. 6A & 6B). Since *N. americana* feed and reproduce on carrion of all sizes and do not display complex parental care, having broad habitat associations likely allows them to take advantage of more carcasses wherever they appear (Anderson and Peck 1985). Furthermore, *N. americana* are the most abundant Silphinae species in southeastern Ontario and are significantly larger than the other common Silphinae species (*Oiceoptoma inaequale* and *O. noveboracense*; Table 1; Anderson and Peck 1985; Ratcliffe 1996; Collard 2018). As such, *N. americana* likely do not face significant competitive pressures from *Nicrophorus*, which are limited to small carcasses, nor from other Silphinae, leaving them unrestricted to occupy all available habitats. *O. inaequale* and *O. noveboracense* also display generalist habitat associations, although previous studies suggest that *O. inaequale* is more abundant in deciduous forest (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995). Both species were most abundant and occurred most often in ground-level traps, but *O. inaequale* also occurred in lower abundance in some canopy-level traps at sites with many red oak trees (Fig. 6C-F). *O. inaequale* and *O. noveboracense* may emerge early in spring to avoid competition with larger carrion beetles such as *N. americana* (Anderson 1982; Anderson and Peck 1985). The
tendency for *O. inaequale* to occupy deciduous forest with many red oaks likely reflects similar reasons as those discussed for *N. sayi*; small vertebrates emerging from winter hibernacula likely congregate near seed-bearing trees like oaks and maples creating concentrated areas of available carrion. It’s unclear why *O. noveboracense* does not display similar associations, however, it may be that at our study site *O. inaequale* is able to outcompete *O. noveboracense* for higher quality forest habitat. In many areas of their distributions; one species is usually rare or absent (Anderson and Peck 1985; Ratcliffe 1996). In our survey, both species were collected and often in the same trap. Yet, over the entire trapping period, we caught four times as many *O. inaequale* as *O. noveboracense* suggesting that *O. inaequale* are at least numerically dominant at our study site (Table 1). Lastly, *Necrodes surinamensis* were rare in our survey and no significant habitat associations were identified with their abundance or occurrence (Fig. 5C & 5D). In nature, *Necrodes surinamensis* seek out large carrion such as deer for reproduction and the adults feed primarily on fly maggots (Ratcliffe 1972; Anderson 1982; Anderson and Peck 1985). Thus, the chicken wings we used to bait our traps may have been insufficient to attract them in large numbers or they may be rare in the area, as has previously been found (Anderson 1982).

**General Patterns of Habitat Use**

The patterns of habitat differences identified among some *Nicrophorus* in southeastern Ontario – in particular, the three habitat specialists (*N. pustulatus, N. hebes, N. marginatus*) - could be the result of a variety of non-mutually exclusive processes. Foremost, competition for limiting resources could influence the distribution of species across habitats (Connell 1961; Ziv et al. 1993; Wisheu 1998). Aggressive interactions among *Nicrophorus* species are highly asymmetric and the outcomes of such interactions are primarily mediated by body size, with
larger beetles typically winning contests for resources (Otronen 1988; Safryn and Scott 2000). Large species such as *N. orbicollis* may be competitively dominant and competitively exclude smaller species from high-quality habitats such as forest (Hardin 1960; Anderson 1982; Trumbo 1990; Ziv et al. 1993). As a result, smaller or less competitive species like *N. pustulatus, N. defodiens, N. hebes*, and *N. marginatus* may be forced into lower quality habitats like wetlands and open fields. To avoid the costs associated with reproducing in low quality habitat, specialist species may have evolved adaptations to their local environments that aid in survival and reproduction or they may possess broader environmental tolerances (Morse 1974; Toft 1985; McPeek 1996; Irschick et al. 1999; Hilton et al. 2008; Dreiss et al. 2012). In contrast, competitively dominant species like *N. orbicollis* may be able to monopolize higher quality habitats, but lack the adaptations or tolerance required to also occupy and persist in lower quality, marginal habitats. Alternatively, *Nicrophorus* species may be deterred from occupying the same habitats due to costs imposed by frequency-dependent increases in parasitism, predation, or disease (Freeland 1983; Martin 1988a, 1988b). Such interactions are poorly described for carrion beetles, and the overall impacts of these selective pressures on populations of carrion beetles are not well understood. Dispersal limitations could also explain patterns of habitat partitioning if species are unable to colonize novel habitats due to distance or physical barriers (MacArthur 1958; Diamond 1975). Yet, the mosaic nature of habitats at our study sites, with different habitats occurring in close proximity, and the ability of carrion beetles to move large distance (Bedick et al. 1999; Attisano and Kilner 2015), suggests that dispersal limitation is unlikely to restrict habitat use at our site. Finally, the habitat differences among carrion beetles could reflect historical factors or have arisen due to chance during a species evolutionary history, and thus not reflect contemporary selective pressures or interactions among co-occurring species.
To identify the specific mechanisms underlying differences in habitat use, we require measures of relative competitive and reproductive performance and tests among these alternative hypotheses (Hairston 1980a; Wisheu 1998; Blanquart et al. 2013). This could be accomplished using reciprocal transplants and removal experiments to examine species’ performance when in different habitats and in the presence or absence of competitor species.

Three other *Nicrophorus* species (*N. orbicollis, N. sayi, N. tomentosus*) overlapped heavily in habitat use but likely partition resources along a different environmental gradient. *N. orbicollis, N. sayi,* and *N. tomentosus* are frequently found in the same habitats and may instead partition resources temporally by separating their reproductive seasons (Anderson 1982; Wilson et al. 1984; Wettlaufer 2019). *N. sayi* is the first *Nicrophorus* species to emerge in the spring and is reproductively active in our region from late April to June (Anderson 1982; Wilson et al. 1984; Anderson and Peck 1985; Wettlaufer 2019). *N. orbicollis* is primarily active in the summer from June to August and is typically the most abundant *Nicrophorus* species during this time (Anderson 1982; Wilson et al. 1984; Anderson and Peck 1985; Wettlaufer 2019). *N. tomentosus* emerges later, with peak numbers from late July to early October (Anderson 1982; Wilson et al. 1984; Anderson and Peck 1985; Wettlaufer 2019). These three species may thus be able to coexist, despite relying on similar resources for reproduction, by partitioning these resources through time (seasons) instead of space (habitat).

Other species that overlap in habitat-use and seasonal activity may reduce shared resource requirements by reproducing on different sizes of carrion (Trumbo 1990, 1992; Ikeda et al. 2006). For example, *N. defodiens* can reproduce on significantly smaller carrion than *N. orbicollis* and thus avoid competition for very small carcasses (Trumbo 1990). In addition, smaller *Nicrophorus* species may be more efficient at exploiting available carrion resources
Smaller species like *N. tomentosus, N. defodiens*, and *N. hebes* are diurnal and become active earlier in the day than their larger, predominantly nocturnal, competitors (Shubeck 1971; Anderson and Peck 1985; Scott 1998). Becoming active earlier may provide an advantage against competitors by allowing these species to find and secure carrion before larger species become active (Trumbo and Bloch 2002). Additionally, these species may be able to hide carcasses from competitors and other scavengers more quickly by submerging carrion into shallow pits under leaf litter rather than fully burying it (Anderson and Peck 1985; Trumbo and Bloch 2002).

The patterns of habitat use that we found in southeastern Ontario mirror those observed in *Nicrophorus* assemblages in other regions of the world. Many *Nicrophorus* species appear to share similar generalist habitat associations and preferences for forested areas as those exhibited by *N. orbicollis* and *N. sayi*. These include the Palearctic species *N. vespilloides, N. maculifrons, N. interruptus, N. sepultor*, and *N. quadripunctatus*, the North American species *N. guttula*, and the Central American species *N. mexicanus* (Anderson and Peck 1985; Růžička 1994; Ratcliffe 1996; Ohkawara et al. 1998; Dekeirsschieter et al. 2011; Urbański and Baraniak 2015; Çiftçi et al. 2018). The widely distributed Holarctic species *N. investigator* appears to display a similar breadth of habitat use as *N. tomentosus*, being found in forests, open habitats, high and low elevations, and the forest canopy (Smith and Heese 1995; Ratcliffe 1996; Ohkawara et al. 1998; Scott 1998; Trumbo and Bloch 2000; Dekeirsschieter et al. 2011; Çiftçi et al. 2018). Like *N. pustulatus*, both *N. investigator* and *N. tenuipes* have been found to be common in the forest canopy in Japan, suggesting that vertical partitioning may be an important axis of resource partitioning among *Nicrophorus* (Ohkawara et al. 1998; Wettlaufer et al. 2018). The broadly distributed Palearctic species *N. humator* shares a preference for coniferous forest, as has been
suggested for *N. defodiens* (Růžička 1994; Scott 1998; Urbaniński and Baraniak 2015; Çiftçi et al. 2018). Likewise, throughout their distribution in northern Europe and East Asia, *N. vespillo* are predominantly associated with open fields similar to *N. marginatus* (Scott 1998; Dekirersschieter et al. 2011; Urbaniński and Baraniak 2015; Çiftçi et al. 2018), but have also been found to be abundant in moist marshland (Růžička 1994), like *N. hebes*. Open-field specialists like *N. marginatus* also appear to be common in other assemblages. Species such as *N. antennatus*, *N. germanicus*, and *N. vestigator* in Europe and Asia, and *N. hybridus*, *N. obscurus* and *N. carolinus* in North America are primarily found in large open fields, meadows, prairies, and steppe habitats (Anderson and Peck 1985; Růžička 1994; Lingafelter 1995; Ratcliffe 1996; Scott 1998; Dekirersschieter et al. 2011; Urbaniński and Baraniak 2015; Çiftçi et al. 2018). Despite these apparent similarities, the habitat associations of many *Nicrophorus* species remain poorly known and only a limited selection of habitats have been surveyed in most regions. Future investigations of the habitat associations of *Nicrophorus* in regions of Europe and Asia may clarify similarities and differences in habitat use among co-occurring *Nicrophorus* species and identify some of the recurrent selective pressures that influence carrion beetles across communities.

In conclusion, we found that co-occurring *Nicrophorus* species in southeastern Ontario differ in their use of habitats in a pattern consistent with habitat partitioning. Our results show that three *Nicrophorus* species have specialist associations with habitats where other *Nicrophorus* species are less common, while another three *Nicrophorus* species exhibit generalist habitat associations and overlap highly in habitat use with other co-occurring species. These *Nicrophorus* species that did not differ in habitat use are those that may instead partition through reproductive timing (Wettlaufer 2019). Our findings suggest that habitat may be an important resource axis along which some *Nicrophorus* species partition, however, other resource axes may
also be important for *Nicrophorus* coexistence. Further investigations will be needed to
determine if habitat partitioning has truly occurred in response to species interactions and to
identify the underlying mechanisms responsible. Nonetheless, our findings represent a crucial
first step towards understanding the role of habitat partitioning in facilitating coexistence
between co-occurring *Nicrophorus* species and furthers our understanding of both how closely
related species coexist and of the processes that ultimately shape local diversity.
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Appendix A: Supplementary Materials

**Table S1.** Names, abbreviations used in analyses, and descriptions of all 55 predictor variables measured in our surveys of local habitat characteristics and used in our statistical analyses. Diameter at breast height is abbreviated as DBH in all relevant descriptions.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trap type</td>
<td>“Trap”</td>
<td>Ground-level or canopy-level lethal pitfall trap; canopy traps were suspended 6m above the ground and were paired with a ground-level trap at each site</td>
</tr>
<tr>
<td>Habitat type</td>
<td>“Habitat”</td>
<td>The type of habitat at each site, based on the dominant vegetation and substrate type. Six categories: deciduous forest, coniferous forest, mixed forest, rocky outcrop, wetland, and open field</td>
</tr>
<tr>
<td>Dominate substrate type</td>
<td>“Substrate”</td>
<td>The most abundant type of substrate at a site. Five categories: loose soil, sandy soil, hard soil, muddy soil, and rock</td>
</tr>
<tr>
<td>Average soil depth (cm)</td>
<td>“Depth”</td>
<td>The average soil depth at a site in centimetres</td>
</tr>
<tr>
<td>Leaf litter depth (cm)</td>
<td>“Litter”</td>
<td>The depth of the leaf litter layer at a site measured in centimetres</td>
</tr>
<tr>
<td>Forest canopy</td>
<td>“Canopy”</td>
<td>Open or closed tree canopy</td>
</tr>
<tr>
<td>Percent ground covered by grass</td>
<td>“Grass”</td>
<td>The percentage of ground in our 2.5m radius plots covered by grass</td>
</tr>
<tr>
<td>Percent ground covered by rock</td>
<td>“Rock”</td>
<td>The percentage of ground in our 2.5m radius plots covered by rock</td>
</tr>
<tr>
<td>Percent ground covered by leaf litter</td>
<td>“Leaf”</td>
<td>The percentage of ground in our 2.5m radius plots covered by leaf litter</td>
</tr>
<tr>
<td>Percent bare ground</td>
<td>“Bare”</td>
<td>The percentage of bare ground in our 2.5m radius plots</td>
</tr>
<tr>
<td>Percent ground covered by sedge</td>
<td>“Sedge”</td>
<td>The percentage of ground in our 2.5m radius plots covered by sedge</td>
</tr>
<tr>
<td>Percent ground covered by shrubs</td>
<td>“Shrub”</td>
<td>The percentage of ground in our 2.5m radius plots covered by shrubs</td>
</tr>
<tr>
<td>Percent ground covered by saplings</td>
<td>“Sapling”</td>
<td>The percentage of ground in our 2.5m radius plots covered by small saplings</td>
</tr>
<tr>
<td>Percent ground covered by brush</td>
<td>“Brush”</td>
<td>The percentage of ground in our 2.5m radius plots covered by brush</td>
</tr>
<tr>
<td>Percent ground covered by ferns</td>
<td>“Fern”</td>
<td>The percentage of ground in our 2.5m radius plots covered by ferns</td>
</tr>
<tr>
<td>Percent ground covered by moss</td>
<td>“Moss”</td>
<td>The percentage of ground in our 2.5m radius plots covered by mosses</td>
</tr>
<tr>
<td>Percent ground covered by marsh vegetation</td>
<td>“Marsh”</td>
<td>The percentage of ground in our 2.5m radius plots covered by marsh vegetation</td>
</tr>
<tr>
<td>Percent ground covered by open water</td>
<td>“Water”</td>
<td>The percentage of ground in our 2.5m radius plots covered by open water</td>
</tr>
</tbody>
</table>
Percent ground covered by fallen logs

Number of sugar maples (Acer saccharum)
Number of white ashes (Fraxinus americana)
Number of white birches (Betula papyrifera)
Number of American beeches (Fagus grandifolia)
Number of eastern white pines (Pinus strobus)
Number of red juniper (Juniperus virginiana)
Number of white ashes (Fraxinus americana)
Number of green ashes (Fraxinus pennsylvanica)
Number of basswoods (Tilia americana)
Number of red oak (Quercus rubra)  
Number of ironwoods (Ostrya virginiana)
Number of white elms (Ulmus americana)
Number of dead trees
Number of red pines (Pinus resinosa)
Number of silver maples (Acer saccharinum)
Number of white oak (Quercus alba)
Number of trembling aspens (Populus tremuloides)
Number of bigtooth aspens (Populus grandidentata)
Number of blue beeches (Carpinus caroliniana)

“Log”
“Sugar.Maple”
“White.Ash”
“White.Birch”
“American.Beech”
“White.Pine”
“Red.Cedar”
“Green.Ash”
“Basswood”
“Red.Oak”
“Ironwood”
“White.Elm”
“Dead”
“Red.Pine”
“Silver.Maple”
“White.Oak”
“Trembling.Aspen”
“Bigtooth.Aspen”
“Blue.Beech”

The percentage of ground in our 2.5m radius plots covered by fallen logs
The number of sugar maples with DBH greater than 9cm counted within our 17.25m radius plots
The number of white ashes with DBH greater than 9cm counted within our 17.25m radius plots
The number of white birches with DBH greater than 9cm counted within our 17.25m radius plots
The number of American beeches with DBH greater than 9cm counted within our 17.25m radius plots
The number of eastern white pines with DBH greater than 9cm counted within our 17.25m radius plots
The number of red junipers with DBH greater than 9cm counted within our 17.25m radius plots
The number of red maples with DBH greater than 9cm counted within our 17.25m radius plots
The number of green ashes with DBH greater than 9cm counted within our 17.25m radius plots
The number of basswoods with DBH greater than 9cm counted within our 17.25m radius plots
The number of red oaks with DBH greater than 9cm counted within our 17.25m radius plots
The number of ironwoods with DBH greater than 9cm counted within our 17.25m radius plots
The number of white elms with DBH greater than 9cm counted within our 17.25m radius plots
The number of dead trees with DBH greater than 9cm counted within our 17.25m radius plots
The number of red pines with DBH greater than 9cm counted within our 17.25m radius plots
The number of silver maples with DBH greater than 9cm counted within our 17.25m radius plots
The number of white oaks with DBH greater than 9cm counted within our 17.25m radius plots
The number of trembling aspens with DBH greater than 9cm counted within our 17.25m radius plots
The number of bigtooth aspens with DBH greater than 9cm counted within our 17.25m radius plots
The number of blue beeches with DBH greater than 9cm counted within our 17.25m radius plots
<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Common Name</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eastern white cedar</td>
<td>“Nothern.White.Cedar”</td>
<td>The number of eastern white cedars with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Thuja occidentalis)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of eastern hemlocks</td>
<td>“Eastern.Hemlock”</td>
<td>The number of eastern hemlocks with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Tsuga canadensis)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of black cherry trees</td>
<td>“Black.Cherry”</td>
<td>The number of black cherry trees with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Prunus serotina)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of shagbark hickory trees</td>
<td>“Shagbark.Hickory”</td>
<td>The number of shagbark hickory trees with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Carya ovata)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of crab apple trees</td>
<td>“Crab.Apple”</td>
<td>The number of crab apple trees with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(genus Malus)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of rock elms</td>
<td>“Rock.Elm”</td>
<td>The number of rock elms with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Ulmus thomasii)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of white spruces</td>
<td>“White.Spruce”</td>
<td>The number of white spruces with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Picea glauca)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of black ashes</td>
<td>“Black.Ash”</td>
<td>The number of black ashes with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Fraxinus nigra)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of yellow birches</td>
<td>“Yellow.Birch”</td>
<td>The number of yellow birches with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Betula alleghaniensis)</td>
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<td></td>
</tr>
<tr>
<td>Number of common buckthorns</td>
<td>“Common.Buckthorn”</td>
<td>The number of common buckthorns with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Rhamnus cathartica)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of pear hawthorns</td>
<td>“Pear.Hawthorn”</td>
<td>The number of pear hawthorns with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Crataegus calpodendron)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of slippery elms</td>
<td>“Slippery.Elm”</td>
<td>The number of slippery elms counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>(Ulmus rubra)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total number of tree species</td>
<td>“Total.Tree.Species”</td>
<td>The total number of tree species identified with DBH greater than 9cm within our 17.25m radius plots</td>
</tr>
<tr>
<td>Total number of trees</td>
<td>“Total.Trees”</td>
<td>The total number of trees with DBH greater than 9cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>Total number of small trees</td>
<td>“Small.Trees”</td>
<td>The total number of trees with DBH between 9cm and 23cm counted within our 17.25m radius plots</td>
</tr>
<tr>
<td>Total number of medium trees</td>
<td>“Medium.Trees”</td>
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</tr>
<tr>
<td>Total number of large trees</td>
<td>“Large.Trees”</td>
<td>The total number of trees with DBH greater than 38cm counted within our 17.25m radius plots</td>
</tr>
</tbody>
</table>