

# Habitat use of co-occurring burying beetles (genus *Nicrophorus*) in southeastern Ontario, Canada

K.W. Burke, J.D. Wettlaufer, D.V. Beresford, and P.R. Martin

**Abstract:** The coexistence of closely related species plays an important role in shaping local diversity. However, competition for shared resources can limit the ability of species to coexist. Many species avoid the costs of coexistence by diverging in habitat use, known as habitat partitioning. We examine patterns of habitat use in seven co-occurring species of burying beetles (genus *Nicrophorus* Fabricius, 1775), testing the hypothesis that *Nicrophorus* species partition resources by occupying distinct habitats. We surveyed *Nicrophorus* abundance and 54 habitat characteristics at 100 random sites spanning an environmentally diverse region of southeastern Ontario, Canada. We found that three species occupied distinct habitat types consistent with habitat partitioning. Specifically, *Nicrophorus pustulatus* Herschel, 1807, *Nicrophorus hebes* Kirby, 1837, and *Nicrophorus marginatus* Fabricius, 1801 appear to be specialists for forest canopy, wetlands, and open fields, respectively. In contrast, *Nicrophorus orbicollis* Say, 1825, *Nicrophorus sayi* Laporte, 1840, and *Nicrophorus tomentosus* Weber, 1801 appear to be generalists with wide breadths of habitat use. We were unable to identify the habitat associations of *Nicrophorus defodiens* Mannerheim, 1846. Our findings are consistent with habitat acting as an important resource axis along which some *Nicrophorus* species partition; however, divergence along other resource axes (e.g., temporal partitioning) also appears important for *Nicrophorus* coexistence.

**Key words:** Silphidae, burying beetles, *Nicrophorus*, habitat, habitat use, habitat partitioning, resource partitioning, species coexistence, niche partitioning, community ecology.

**Résumé :** La coexistence d'espèces étroitement apparentées joue un important rôle dans la modulation de la diversité locale. La concurrence pour des ressources communes peut toutefois limiter la capacité d'espèces à coexister. De nombreuses espèces évitent les coûts de la coexistence en faisant des utilisations divergentes de l'habitat, un phénomène appelé partitionnement de l'habitat. Nous examinons les motifs d'utilisation de l'habitat chez sept espèces cooccurrentes de coléoptères fousseurs (genre *Nicrophorus* Fabricius, 1775), afin de vérifier l'hypothèse voulant que les espèces de *Nicrophorus* se partitionnent les ressources en occupant des habitats distincts. Nous avons évalué l'abondance de *Nicrophorus* et 54 caractéristiques de l'habitat en 100 sites choisis aléatoirement couvrant une région du sud-est de l'Ontario (Canada) d'une grande diversité environnementale. Nous avons constaté que trois espèces occupent des types d'habitats distincts, ce qui concorde avec un partitionnement de l'habitat. Plus précisément, *Nicrophorus pustulatus* Herschel, 1807, *Nicrophorus hebes* Kirby, 1837 et *Nicrophorus marginatus* Fabricius, 1801 semblent être des spécialistes du couvert forestier, des terres humides et des champs ouverts, respectivement. En revanche, *Nicrophorus orbicollis* Say, 1825, *Nicrophorus sayi* Laporte, 1840 et *Nicrophorus tomentosus* Weber, 1801 semblent être des généralistes caractérisés par de vastes gammes d'utilisations de l'habitat. Nous n'avons pas été en mesure de cerner les associations d'habitat de *Nicrophorus defodiens* Mannerheim, 1846. Nos constatations concordent avec l'interprétation voulant que l'habitat constitue un important axe de ressources le long duquel certaines espèces de *Nicrophorus* se répartissent, bien que des divergences le long d'autres axes de ressources (p. ex. un partitionnement dans le temps) semblent aussi être importantes pour la coexistence des *Nicrophorus*. [Traduit par la Rédaction]

**Mots-clés :** silphidés, coléoptères fousseurs, *Nicrophorus*, habitat, utilisation de l'habitat, partitionnement de l'habitat, partitionnement des ressources, coexistence d'espèces, partitionnement des niches, écologie des communautés.

## Introduction

The coexistence of closely related species with similar ecologies is thought to play an important role in shaping patterns of biodiversity. Closely related species make up a large component of local diversity and the interactions between them exert a strong influence on community organization (Toft 1985; Wright 2002; Siepielski and McPeck 2010; Burns and Strauss 2011), the evolution of species traits (Brown and Wilson 1956; Grant and Grant 2006), and rates of diversification (Richman and Price 1992; Price et al. 2014). However, the coexistence of similar species is paradoxical because competition for shared resources should cause most eco-

logically similar species to be excluded from a community (Gause 1932; Hardin 1960; Violle et al. 2011). To coexist, co-occurring species are thought to require divergence in their resource use, reducing the frequency of competitive interactions (Brown and Wilson 1956; Schoener 1974; Losos 1994). Understanding how coexisting species use different resources is thus important for understanding how and when closely related species can coexist.

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; Grace and Wetzel 1981; Albertson 2008).

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Habitat partitioning is common among co-occurring taxa around the world (Diamond 1973; Schoener 1974; Toft 1985; Wisheu 1998) and is thought to be an important early step in species divergence and trait evolution (Richman and Price 1992; Stuart et al. 2014; 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 way species diverge in resource use, occurring significantly more often and producing larger differences in resource use than either the partitioning of time or resource types, such as food or nesting sites (Schoener 1974, 1986; Toft 1985). Habitat is also thought to often be the first resource axis along which allopatric species diverge upon secondary contact (Richman and Price 1992; Schluter 2000; Freeman 2015), possibly due to the wide availability of diverse habitat gradients, and that, unlike when partitioning time or resource types, partitioning habitat often does not require complex physiological or morphological adaptations. Habitat partitioning may be crucial for facilitating species coexistence; however, few general rules have been identified governing how and when habitat partitioning occurs (Schoener 1974; Toft 1985) and its role in facilitating species coexistence relative to other forms of resource partitioning is currently not well understood.

In southeastern Ontario, Canada, seven species of burying beetle (subfamily Nicrophorinae; genus *Nicrophorus* Fabricius, 1775) co-occur despite all requiring a shared, limiting resource for reproduction. These species include *Nicrophorus orbicollis* Say, 1825, *Nicrophorus sayi* Laporte, 1840, *Nicrophorus tomentosus* Weber, 1801, *Nicrophorus pustulatus* Herschel, 1807, *Nicrophorus hebes* Kirby, 1837 (previously known as *Nicrophorus vespilloides* Herbst, 1783; Sikes et al. 2016), *Nicrophorus marginatus* Fabricius, 1801, and *Nicrophorus defodiens* Mannerheim, 1846 (Anderson 1982; Anderson and Peck 1985; Beninger and Peck 1992; Robertson 1992). All burying beetle species require small vertebrate carrion for reproduction, which they often bury and use as a food source and nest for developing larvae (Pukowski 1933; Wilson and Fudge 1984; Anderson and Peck 1985; Scott 1998; Smith et al. 2007). 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 are thought to have evolved to partition resources along temporal and spatial gradients, including occupying distinct habitats (Anderson 1982; Wilson et al. 1984; Beninger and Peck 1992; Keller et al. 2019). Therefore, investigations into how and when co-occurring *Nicrophorus* species use habitats differently could further our understanding of the role habitat partitioning plays in facilitating coexistence among closely related species.

Previous studies have described the broad habitat associations of *Nicrophorus* species throughout their distributions. *Nicrophorus 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 1998; Trumbo and Bloch 2000; Keller et al. 2019). 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 in 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). Meanwhile, *N. hebes* have been found almost exclusively in wetland habitats such as *Sphagnum* L. bogs and cattail marshes, occasionally occurring in other wetland-bordering habitats (Anderson 1982; Anderson and Peck 1985; Beninger 1989, 1994; Beninger and Peck 1992; Sikes et al. 2016). *Nicrophorus marginatus* likewise 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; Keller et al. 2019). Lastly, *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).

If habitat partitioning facilitates the coexistence of *Nicrophorus* species, then we predicted that co-occurring *Nicrophorus* species in southeastern Ontario should use distinct habitats within our focal study site (~2700 ha reserve). We tested this prediction by conducting intensive field surveys to quantify burying beetle abundance and habitat characteristics. Our study improves upon previous work by examining the associations between *Nicrophorus* species, trap height (ground versus forest canopy), and 54 local habitat characteristics related to substrate and vegetative properties at random sampling sites within an environmentally diverse and heterogeneous region of southeastern Ontario where seven *Nicrophorus* species co-occur.

## Materials and methods

### Site description

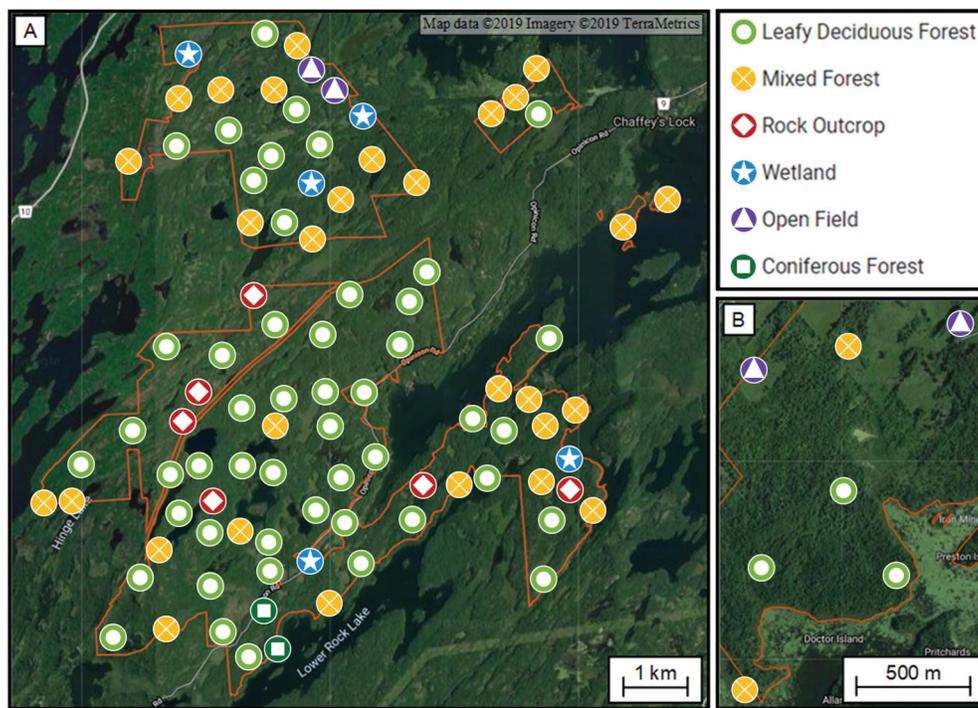
We surveyed burying beetle abundance and measured local habitat characteristics at 100 random sampling sites (detailed below), spanning the properties of the Queen's University Biological Station (QUBS; 44.5653°N, 76.322°W; 129 m above sea level), near Elgin, Ontario, Canada (Figs. 1A and 1B). These sites have been previously used for a variety of long-term studies and were originally selected by randomly generating GPS coordinates within the QUBS property boundaries with the criteria that sites be at least 400 m apart and not be in open water. The resultant sites spanned an area over 2690 ha in size across a 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 open fields.

### Survey of burying beetle abundance

We surveyed burying beetle abundance between 16 April and 29 October 2017 using lethal pitfall traps set for 7 days at a time (Wettlaufer et al. 2018). At each sampling site, we simultaneously set one ground-level trap and a second canopy-level trap hung 6 m above from a nearby tree branch. Our traps consisted of yellow plastic buckets 35 cm deep and 17 cm wide filled to approximately 15 cm with saturated saline water and baited with chicken wings wrapped in cheesecloth (Supplementary Fig. S1).<sup>1</sup> Prior to deployment, the chicken wings were kept frozen without thawing or ripening. We suspended the chicken wings above the saline solu-

<sup>1</sup>Supplementary material (tables, figures, and text) are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2019-0287>.

**Fig. 1.** (A) Map of the 100 randomly generated sampling sites where we conducted our surveys of burying beetle (genus *Nicrophorus*) abundance and local habitat characteristics on the main properties of the Queen's University Biological Station (QUBS). All sites are at least 400 m apart and do not fall within bodies of water. (B) Sampling sites located on the Bracken tract properties of QUBS. Sites are coded by color and symbols 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. The figure was created in Google Maps. Base map from Google and TerraMetrics, courtesy of Google. Shape file of boundaries of the QUBS property was provided by the Queen's University Biological Station. Color version online.



tion by wrapping a piece of steel craft wire around the chicken and attaching it to the center of a 35 cm<sup>2</sup> square of chicken wire placed over the opening of the bucket. To prevent rainfall from entering the bucket, we covered each trap with a 30 cm<sup>2</sup> plywood board elevated slightly above the bucket's lip. For ground traps, we placed large stones on top of the board to deter vertebrate scavengers from disturbing the traps. We set traps at all our sites over three 4-week periods; 16 April to 24 May, 4 June to 12 July, and 24 July to 25 August. We also trapped at 44 of our sites a fourth time between 8 September and 29 October 2017. We collected all burying beetles and identified them to species and sex following Anderson and Peck (1985).

#### Survey of local habitat characteristics

We conducted surveys of local habitat characteristics at each site following a modified version of the Breeding Biology Research and Monitoring Database (BBird) field protocol for measuring vegetation (Martin et al. 1997). Originally designed for describing bird nesting sites, the BBird protocols provided us with comprehensive standardized methods for measuring quantitative ground cover and vegetation characteristics.

#### Ground cover, leaf litter, and soil characteristics

At each sampling site, we established a circular 2.5 m radius plot by measuring 2.5 m from the ground-level trap in the four cardinal directions and marking these points with trail flagging tape to signify the edges of the plot. We halved the radius specified in the BBird protocol (5 m) to improve the accuracy of our estimates of ground cover types (Martin et al. 1997). We categorized ground cover within the plot into 13 categories and estimated the relative percentage of plot area covered by each (Supplementary Table S1).<sup>1</sup> To measure leaf litter depth, we dug a small 20 cm deep hole near the center of the plot 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 1.5 m 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 mean soil depth for the site and recorded the most common soil type observed (hard soil, loose soil, muddy soil, sandy soil, or rock).

#### Habitat type, tree species diversity, and tree size

To examine the number and types of trees at each sampling site, we established a circular 17.25 m radius plot centered on each ground-level trap. We aligned the radius of our plots to those used for concurrent LiDAR (light detection and ranging) measures taken at the same locations (P.M. Treitz, personal communication, 2017). We measured 17.25 m 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 9 cm. We then categorized the forest canopy as open or closed based on whether there was tree cover above the center of the plot. We also placed each site into one of six general habitat categories based on the dominant vegetation and substrate type (Supplementary Table S1).<sup>1</sup> 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 23 cm DBH), medium-sized (23 to 38 cm DBH), and large (>38 cm DBH) trees counted within the plot.

#### Statistical analyses

Prior to analyses, we removed any traps that were disturbed by vertebrate scavengers from the data set. For our statistical analy-

**Table 1.** Counts of burying beetles collected in ground-level and canopy-level traps between April and October 2017 during our survey of burying beetle species abundance on the properties of the Queen's University Biological Station.

Nicrophorinae species	Ground-level traps		Canopy-level traps		Total	
	Number of individuals	Number of traps	Number of individuals	Number of traps	Number of individuals	Number of traps
<i>Nicrophorus orbicollis</i>	3565	180	875	127	4440	307
<i>Nicrophorus sayi</i>	629	138	268	95	897	233
<i>Nicrophorus tomentosus</i>	1714	99	1905	109	3619	208
<i>Nicrophorus pustulatus</i>	37	16	491	102	528	118
<i>Nicrophorus defodiens</i>	10	8	4	4	14	12
<i>Nicrophorus hebes</i>	83	21	22	17	105	38
<i>Nicrophorus marginatus</i>	3	1	0	0	3	1
<b>Total</b>	<b>6041</b>	<b>277</b>	<b>3565</b>	<b>327</b>	<b>9606</b>	<b>604</b>

ses, we calculated the mean abundance of each burying beetle species in the ground and canopy traps for each site over the entire trapping period. We used these values as our measure of burying beetle abundance at each site, with ground and canopy traps handled separately.

### 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 (Hothorn and Zeileis 2015). 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 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 based on the degree to which the variable reduces uncertainty in the classification. The predictor variable with the lowest significance value is then used to split the data provided that the 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. The final decision tree produced visualizes the hierarchical relationships between all significant predictors and the response variable, including any interactions between predictor variables.

Conditional inference trees hold several advantages over other common statistical modelling techniques. Classification and regression tree methods like conditional inference trees often perform better, with greater prediction accuracy, than other predictive analyses such as logistic regression models and linear discriminant analysis (Hothorn et al. 2006; Cutler et al. 2007). Conditional inference trees also do not make prior statistical assumptions on the distributions of either response or explanatory variables and can accommodate large numbers of predictor variables. They are robust to non-linearity, multi-collinearity, and interactions between explanatory variables (Hothorn et al. 2006; Olden et al. 2008). Furthermore, while other recursive partitioning tree methods can suffer from issues of overfitting and selection bias towards variables with many possible splits or missing values, conditional inference trees avoid these issues by implementing predetermined stopping criterion in the form of significance tests (Hothorn et al. 2006). The result is a highly accurate and robust statistical method for testing and visualizing hierarchical relationships between a single response variable and multiple predictors. A caveat of conditional inference trees, however, is that the

exact values of quantitative splits in explanatory variables are dependent on the data provided and should be considered only approximations of real biological relationships or thresholds (Johnstone et al. 2014).

In our conditional inference trees, we used the mean abundance of each species in ground and canopy traps at each site as the response variable and trap type (ground or canopy) and all 54 measured habitat characteristics as the predictor variables. Including all 54 habitat variables and trap type (ground or canopy) 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 burying 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.

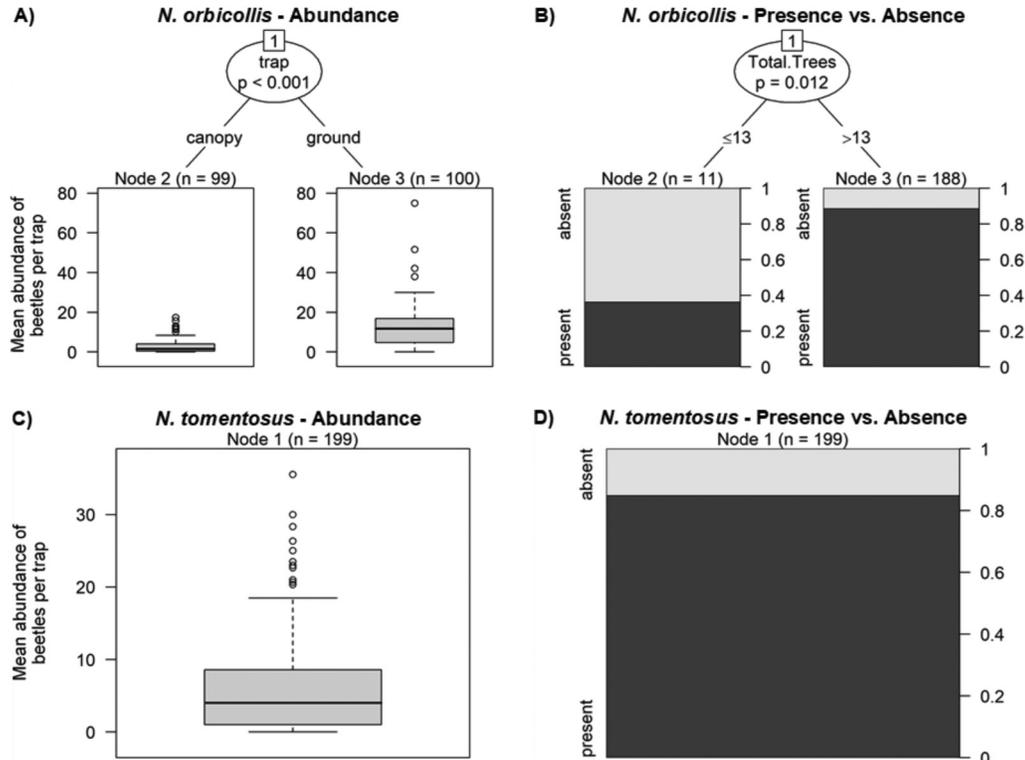
### Results

In total, we collected 9606 burying beetles in 604 successful trapping events with all seven *Nicrophorus* species represented (Table 1). In addition, we collected 3547 beetles belonging to four carrion beetle species in the subfamily Silphinae (Supplementary Table S2):<sup>1</sup> *Necrophila americana* (Linnaeus, 1758), *Oiceoptoma inaequale* (Fabricius, 1781), *Oiceoptoma noveboracense* (Forster, 1771), and *Necrodes surinamensis* (Fabricius, 1775). We include analyses and discussion on the habitat associations of these four Silphinae species in the Supplementary material.<sup>1</sup>

### Habitat associations of burying 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 six *Nicrophorus* species. However, we were unable to identify the habitat associations of *N. defodiens*. Most *N. orbicollis* were caught in ground-level traps ( $n = 100$  traps; Fig. 2A) and traps at sites with many trees ( $n = 188$  traps; Fig. 2B). Most *N. sayi* were caught at sites with many trees ( $n = 188$  traps; Fig. 3B) and were most abundant in ground-level traps at sites with deeper leaf litter ( $n = 16$  traps). At sites with shallow leaf litter, *N. sayi* was more abundant at sites with more red oaks (*Quercus rubra* L.) ( $n = 13$  traps); if red oaks were uncommon, then *N. sayi* was more abundant at sites with more sugar maples (*Acer saccharum* Marsh.) ( $n = 18$  traps); if red oaks and sugar maples were uncommon, then *N. sayi* was more abundant at sites with more eastern white pines (*Pinus strobus* L.) ( $n = 7$  traps); if red oaks, sugar maples, and white pines were uncommon, then *N. sayi* was more abundant at sites with more small trees ( $n = 14$  traps; Fig. 3A). *Nicrophorus tomentosus* were not associated with any of the habitat characteristics that we

**Fig. 2.** Conditional inference trees showing significant associations between local habitat characteristics and (A) *Nicrophorus orbicollis* mean abundance, (B) *N. orbicollis* occurrence, (C) *Nicrophorus tomentosus* mean abundance, and (D) *N. tomentosus* occurrence. Box plots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. The *n* values indicate the number of traps (ground and canopy) included in each node. *Nicrophorus 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.



measured and were abundant ( $n = 199$  traps; Fig. 2C) and present ( $n = 199$  traps; Fig. 2D) in most traps. *Nicrophorus pustulatus* were most abundant ( $n = 100$  traps; Fig. 4A) and most likely to be present ( $n = 100$  traps; Fig. 4B) in canopy-level traps. *Nicrophorus hebes* were most abundant in traps set within wetlands ( $n = 9$  traps; Fig. 4C); however, they were absent from most traps overall. *Nicrophorus hebes* presence was not associated with any specific habitat characteristics ( $n = 199$  traps; Fig. 4D). *Nicrophorus marginatus* were most abundant ( $n = 8$  traps; Fig. 4E) and captured most often ( $n = 8$  traps; Fig. 4F) in traps set within open fields. *Nicrophorus defodiens* were not associated with any habitat characteristics and were instead rare or absent in most traps ( $n = 199$  traps; Figs. 5A and 5B).

## Discussion

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. Using survey data on burying beetle abundance, occurrence, and local habitat characteristics collected from random sampling sites spanning an environmentally diverse region of southeastern Ontario, we find evidence that some co-occurring *Nicrophorus* species differ in their habitat use in a pattern consistent with habitat partitioning. The patterns we identify suggest that the burying 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. 6).

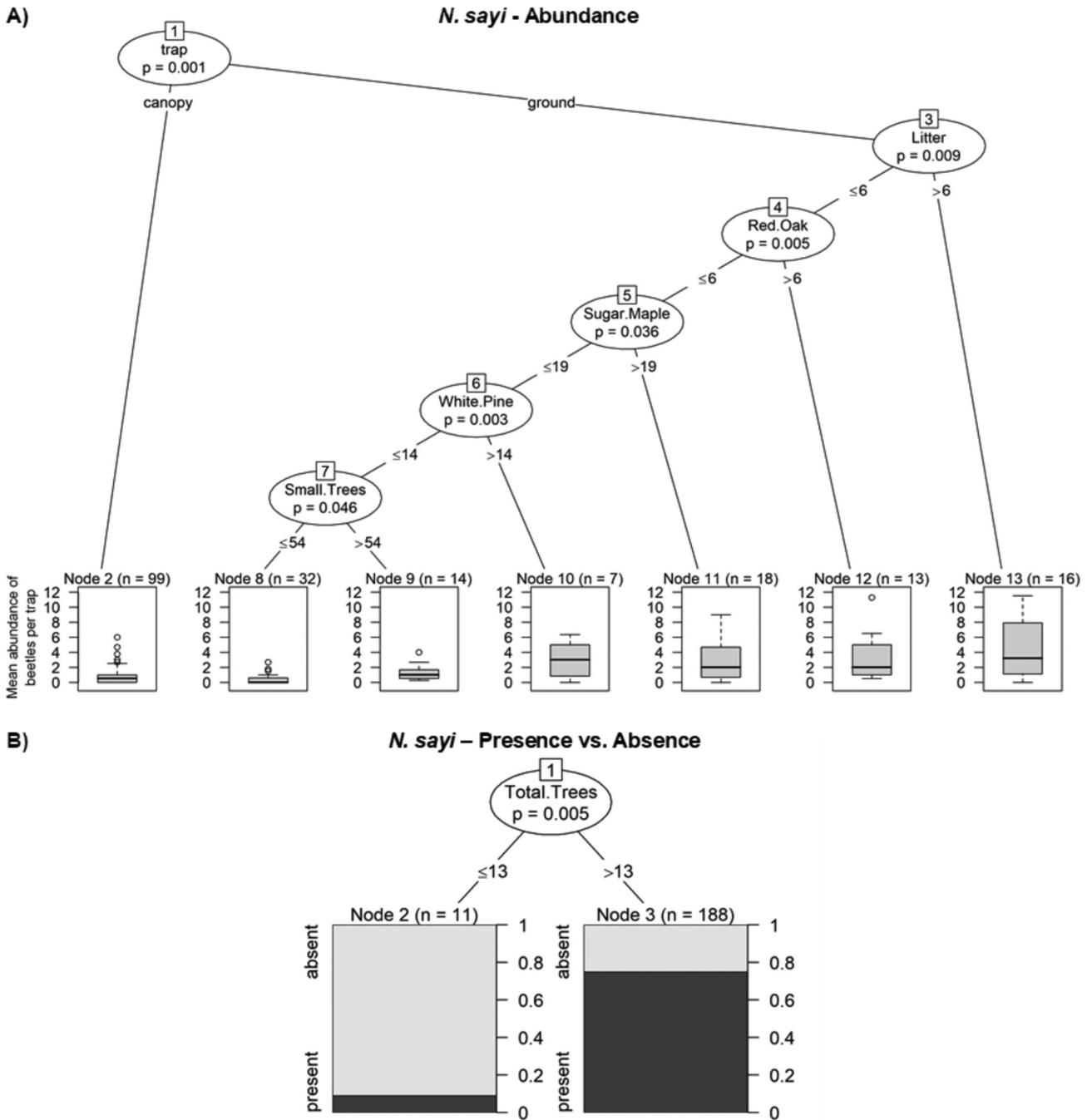
### Nicrophorinae habitat generalists

We found *N. orbicollis* and *N. sayi* to be forest generalists that occur across a variety of habitats, but they seem to prefer dense

forests. *Nicrophorus orbicollis* were abundant in most ground-level traps, regardless of habitat, but they occurred most often at densely forested sites with many trees (Figs. 2A and 2B). Similarly, *N. sayi* were most abundant and common at forested sites with deep leaf litter layers and densely populated with red oaks, sugar maples, white pine, and other small trees (Figs. 3A and 3B). Forests may represent high-quality habitat for burying beetles. Forests commonly contain rich alluvial and sandy loam soils with high organic content (i.e., leaf litter) that are preferred by some *Nicrophorus* species (e.g., *N. orbicollis*; Muths 1991; Bishop et al. 2002; Willemssens 2015). In addition, forest canopy can have a moderating effect on ambient temperature, humidity, and UV radiation (Grimmond et al. 2000; Renaud et al. 2011; Von Arx et al. 2012) that may help maintain optimal conditions for beetle activity and larval development (Smith and Heese 1995; Meierhofer et al. 1999; Nisimura et al. 2002; Merrick and Smith 2004). Meanwhile, trees like red oaks, sugar maples, and white pines produce seeds consumed by many small vertebrates; therefore, the areas around them may act as hot spots of small vertebrate activity and increased carrion availability (Miller and Getz 1977; Dueser and Shugart 1978; Pyare et al. 1993; Schnurr et al. 2004).

*Nicrophorus tomentosus* exhibit the greatest breadth of habitat use among the *Nicrophorus* species of southeastern Ontario; they were present and abundant at the majority of our sampling sites and displayed no associations to any specific habitat characteristics (Figs. 2C and 2D). As has previously been found, *N. tomentosus* appear to be habitat generalists with broad environmental tolerances that allow them to thrive in many different habitats (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995; Lomolino et al. 1995; McPeck 1996; Ratcliffe 1996; Scott 1998; Trumbo and Bloch 2000).

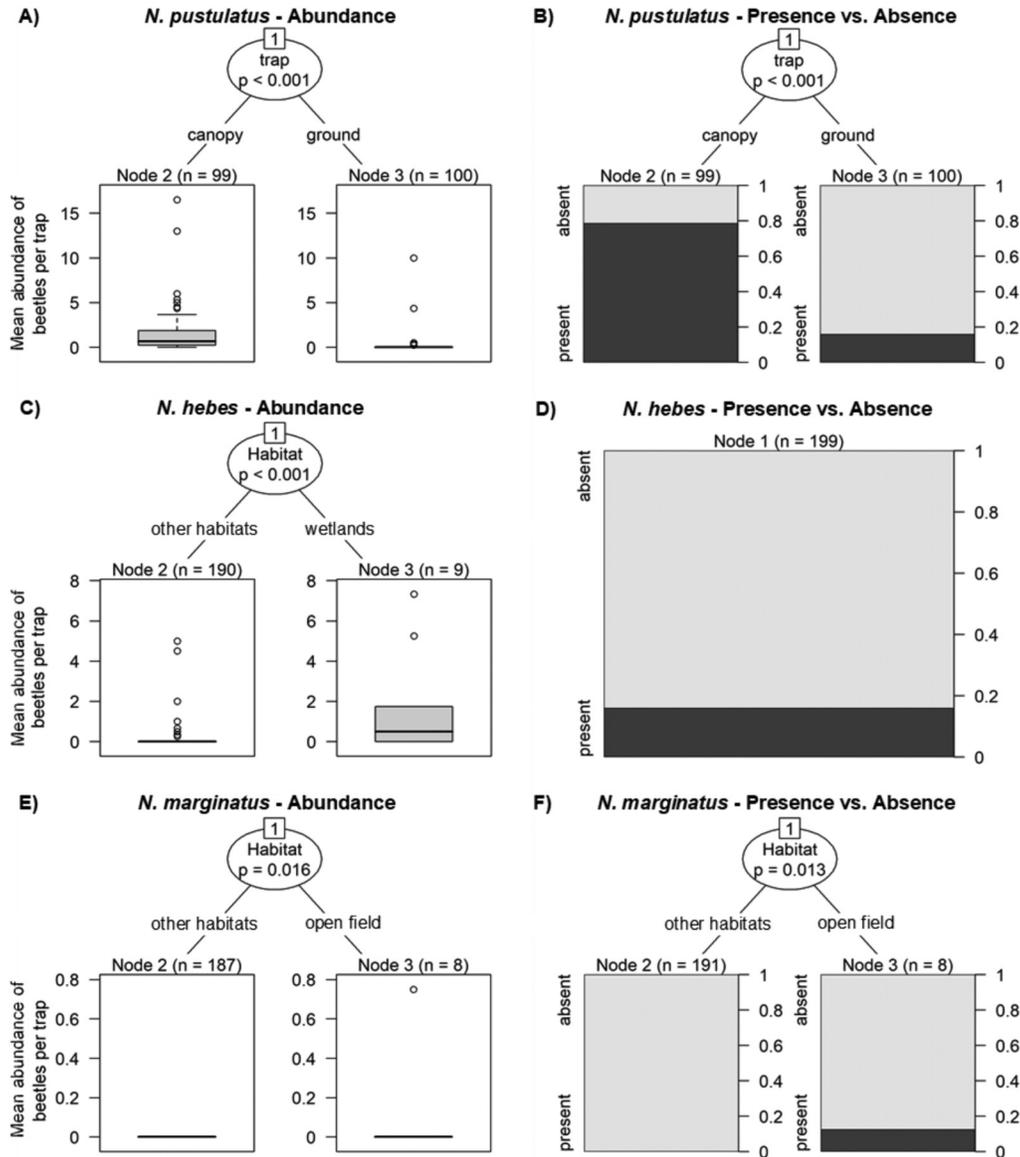
**Fig. 3.** Conditional inference trees displaying significant associations between (A) *Nicrophorus sayi* mean abundance and (B) *N. sayi* occurrence and local habitat characteristics. Box plots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. The *n* values indicate the number of traps (ground and canopy) included in each node. *Nicrophorus sayi* abundance was greater in ground-level traps at sites with deeper leaf litter. At sites with shallow leaf litter, *N. sayi* was more abundant at sites with more red oaks (*Quercus rubra*); if red oaks were uncommon, then *N. sayi* was more abundant at sites with more sugar maples (*Acer saccharum*); if red oaks and sugar maples were uncommon, then *N. sayi* was more abundant at sites with more eastern white pines (*Pinus strobus*); if red oaks, sugar maples, and white pines were uncommon, then *N. sayi* was more abundant at sites with more small trees. *Nicrophorus sayi* were present (dark shading) in a greater number of traps at sites with many trees.



It is important to note, however, that habitats and carrion resources used for feeding can differ from those used for reproduction (Wilson and Knollenberg 1984; Wilson et al. 1984). Competition among *Nicrophorus* occurs primarily for shared reproductive resources, not food resources (Scott 1998). Species should only partition habitats where they seek reproductive resources and may be less restricted in the habitats that they occupy while seek-

ing food (Lomolino et al. 1995). Baited pitfall traps, like we used, do not distinguish between beetles trapped seeking food resources versus those seeking breeding resources and can under-represent breeding individuals if the bait used is unattractive to reproductive beetles (Wilson et al. 1984). As a result, the patterns of habitat use that we identify here may encompass beetles occurring in habitats both for feeding and for reproduction. Our results

**Fig. 4.** Conditional inference trees displaying significant associations between local habitat characteristics and (A) *Nicrophorus pustulatus* mean abundance, (B) *N. pustulatus* occurrence, (C) *Nicrophorus hebes* mean abundance, (D) *N. hebes* occurrence, (E) *Nicrophorus marginatus* mean abundance, and (F) *N. marginatus* occurrence. Box plots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. The *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. *Nicrophorus hebes* abundance was greater in traps located in wetland habitats, whereas *N. hebes* occurrence was not significantly associated with any habitat characteristics. *Nicrophorus marginatus* abundance and presence (dark shading) were greater in traps located in open-field habitat.



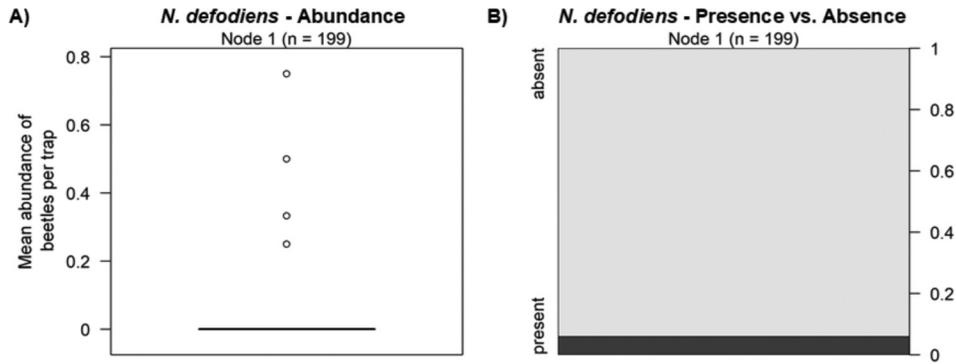
may therefore reflect broader patterns of habitat use than those that occur in nature, in particular, the habitat generalists that we identify may be more restrictive in where they breed.

### Nicrophorinae habitat specialists

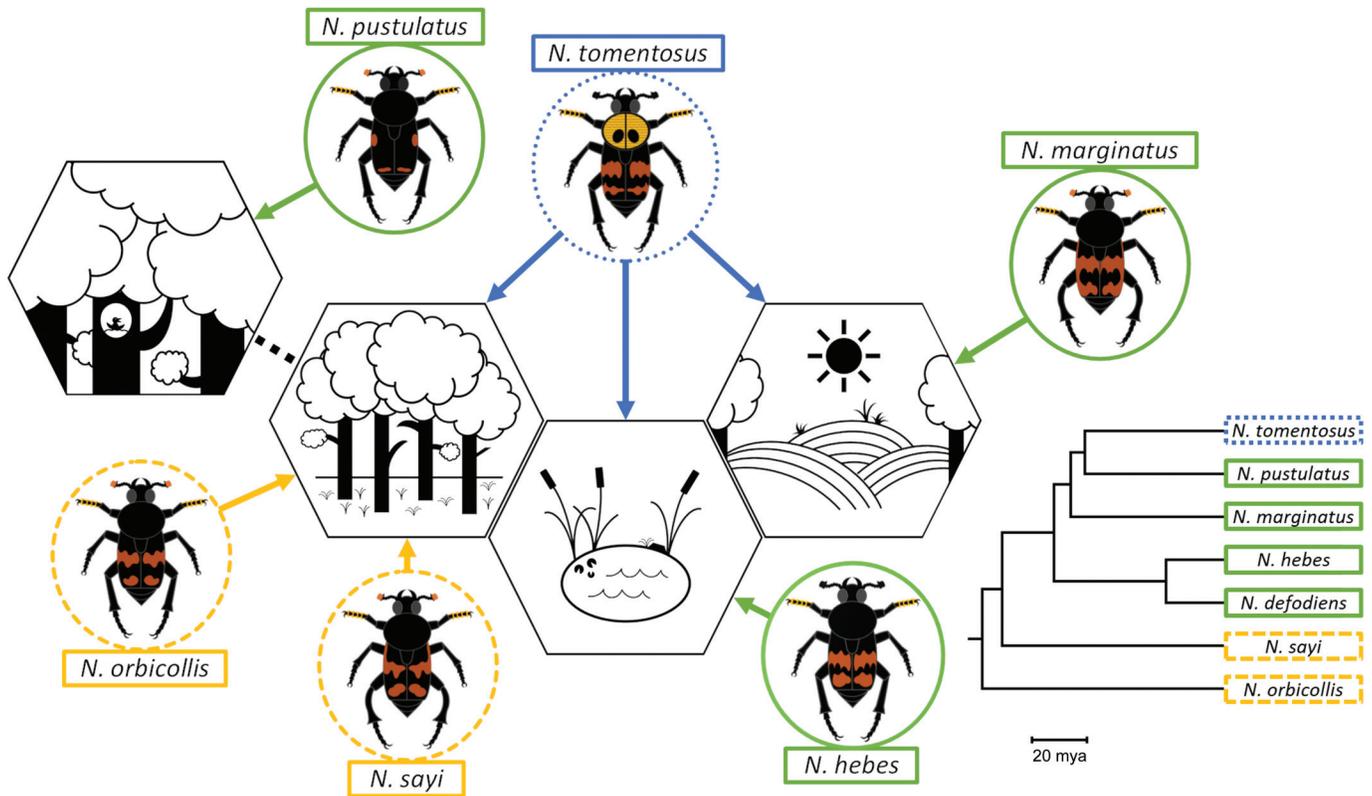
We found *N. pustulatus*, *N. hebes*, and *N. marginatus* to be habitat specialists associated exclusively with specific types of habitat. In our analyses, we found *N. pustulatus* abundance and occurrence were predicted solely by traps in the forest canopy (Figs. 4A and 4B). These findings support the idea that *N. pustulatus* are forest-canopy specialists and that their apparent rarity in previous surveys may be due to their being less likely to be captured in the ground-level pitfall traps typically used to capture burying beetles (Ulyshen et al. 2007; LeGros and Beresford 2010; Lowe and Lauff 2012; Dyer and Price 2013; Wettlaufer et al. 2018). *Nicrophorus hebes*

appear to specialize in occupying wetland habitats, supporting the findings of previous studies (Anderson 1982; Beninger and Peck 1992; Sikes et al. 2016); we found that they were more abundant in wetland habitats than in all other habitat types combined (Fig. 4C). *Nicrophorus hebes* occurrence, however, was not associated with any habitat characteristics (Fig. 4D), possibly due to our capturing them in other habitats bordering wetlands. We captured *N. marginatus* exclusively in open fields (Figs. 4E and 4F), suggesting that they are habitat specialists for open habitats such as meadows and fields, consistent with existing literature on *N. marginatus* habitat use (Anderson 1982; Anderson and Peck 1985; Lingafelter 1995; Lomolino et al. 1995; Ratcliffe 1996; Dyer and Price 2013; Keller et al. 2019). Our *N. marginatus* results, however, are based on only three *N. marginatus* individuals caught in a single

**Fig. 5.** Conditional inference trees displaying significant associations between local habitat characteristics and (A) *Nicrophorus defodiens* mean abundance and (B) *N. defodiens* occurrence. Box plots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. The *n* values indicate the number of traps (ground and canopy) included in each node. No significant associations were identified between any habitat variables and mean abundance or occurrences of *N. defodiens*.



**Fig. 6.** Habitat associations of six co-occurring *Nicrophorus* species in southeastern Ontario, Canada. From left to right, habitats depicted are forest canopy, forest, wetland, and open field. Species are coded by color and line type to represent the breadth of their habitat use: blue and short dash indicates a habitat generalist; yellow and long dash indicates a forest generalist; green and solid line indicates a habitat specialist. A trimmed molecular phylogeny is provided in the lower right corner with breadth of habitat use also indicated by color and line type. This phylogeny was reproduced using published data from Dobler and Müller (2000), Ikeda et al. (2012), and Sikes and Venables (2013). The habitat associations of *Nicrophorus defodiens* are not depicted because too few were captured in our survey to identify significant associations. However, previous research has found *N. defodiens* to be associated with dry coniferous forest (Anderson 1982; Anderson and Peck 1985). Color version online.



trap (Table 1). Our inability to capture *N. marginatus* in large numbers may stem from a lack of their preferred habitat, since they have previously been shown to prefer open habitats greater than 25 ha in size (Trumbo and Bloch 2000) and such large fields are rare at our study site.

**Unidentified habitat associations**

We were unable to identify the habitat associations of *N. defodiens*. This species was rare or absent in most traps, regardless of the surrounding environment (Figs. 5A and 5B). Our inability to iden-

tify the habitat associations of *N. defodiens* may be due to capturing only a few individuals scattered across numerous sampling sites with varying habitat characteristics. During our sampling period, we collected 14 *N. defodiens* at 10 different sites (Table 1). Previous studies report strong associations between *N. defodiens* and forested habitats, with a possible preference for dry coniferous forest (Anderson 1982; Anderson and Peck 1985; Trumbo and Bloch 2000). Coniferous forest is uncommon at our study site (only two of our trapping sites were located within coniferous forest;

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Fig. 1A); therefore, a lack of preferred habitat may explain the rarity of *N. defodiens* in our survey. These findings could indicate that *N. defodiens* are rare habitat generalists; however, it is more likely that they are generally rare in southeastern Ontario, since other carrion beetle surveys have also found them to be uncommon in the region (Anderson 1982; Robertson 1992).

### 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 thought to be highly asymmetric and the outcomes of such interactions are primarily mediated by body size, with larger beetles typically winning contests for carrion (Otronen 1988; Safrin and Scott 2000). Larger species, such as *N. orbicollis* and *N. sayi*, may exclude smaller or less competitive species, such as *N. pustulatus* and *N. hebes*, from higher quality habitats and force them into lower quality, marginal habitats like forest canopies and wetlands (Hardin 1960; Anderson 1982; Trumbo 1990; Ziv et al. 1993). To avoid the costs associated with occupying lower quality habitats, smaller species may have evolved adaptations to their environments that aid in survival and reproduction, or they may possess broader environmental tolerances (Morse 1974; Toft 1985; McPeck 1996; Irschick and Losos 1999; Hilton et al. 2008; Dreiss et al. 2012). For example, *N. pustulatus* may possess greater flight maneuverability for navigating forest canopies while searching for carrion (Wettlaufer et al. 2018), or *N. hebes* may possess tolerance to hypoxic conditions necessary to survive in oxygen-limited and water-saturated wetland soils (Hoback and Stanley 2001; Cavallaro et al. 2017). In contrast, large, competitively dominant species like *N. orbicollis* may be able to monopolize higher quality habitats, such as forest, but lack the adaptations or environmental tolerances required to expand into and persist in more challenging, lower quality habitats.

Alternatively, *Nicrophorus* species may be deterred from sharing habitats due to costs imposed by frequency-dependent increases in parasitism, predation, or disease (Freeland 1983; Martin 1988a, 1988b). However, such interactions are poorly described for burying beetles, and the overall impacts of these selective pressures on burying beetle populations are not well understood. Dispersal limitations could also explain patterns of habitat use 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 site, with different habitats occurring in close proximity, and the ability of burying beetles to move large distance (Bedick et al. 1999; Attisano and Kilner 2015) suggest that dispersal limitation is unlikely to restrict habitat use at our site. Finally, the habitat differences among burying beetles could reflect historical factors or have arisen due to chance during the evolutionary history of the species and thus may not reflect contemporary selective pressures or interactions among co-occurring species (Connell 1980; Vellend 2010). To identify the mechanisms underlying differences in habitat use, we require measures of relative fitness and explicit tests among these alternative hypotheses (Hairston 1980; Wisheu 1998; Blanquart et al. 2013). This could be accomplished using reciprocal transplants and removal experiments to examine the performance of a species when in different habitats and when in the presence or absence of competitor species. It would also be interesting to use phylogenetic analyses to examine the evolution of habitat use among these co-occurring species of *Nicrophorus*.

The three habitat-generalist *Nicrophorus* species overlap heavily in habitat use but likely avoid competing by partitioning resources along a different environmental gradient. *Nicrophorus*

*orbicollis*, *N. sayi*, and *N. tomentosus* are frequently found in the same habitats and are instead thought to partition resources temporally by separating their reproductive seasons (Anderson 1982; Wilson et al. 1984; Wettlaufer 2019). *Nicrophorus sayi* emerges early in the spring and is reproductively active 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 (Anderson 1982; Wilson et al. 1984; Anderson and Peck 1985; Wettlaufer 2019), and *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 *Nicrophorus* species with overlapping habitat use may co-occur by feeding and reproducing on different sizes and types of carrion resources. For example, *N. defodiens*, the smallest *Nicrophorus* species in southeastern Ontario (Collard 2018), can reproduce on very small carcasses (4–6 g) that are often rejected by larger species such as *N. orbicollis* (Trumbo 1990). Likewise, *Nicrophorus americanus* Olivier, 1790, a very large species not found in southeastern Ontario, can reproduce on carcasses that are too large for other species to bury and prepare (80–300 g) and may reject smaller carrion used by other *Nicrophorus* (Kozol et al. 1988). By using carrion outside the size range used by other *Nicrophorus*, both these species, as well as others like them, may avoid competition for essential reproductive resources. Similarly, *N. pustulatus* have uniquely been observed to reproduce on the eggs of oviparous snakes and may avoid competing with other *Nicrophorus* for other types of vertebrate carrion entirely (Blouin-Demers and Weatherhead 2000; Smith et al. 2007; Brown and Beresford 2016). The feeding and reproductive host preferences of many *Nicrophorus* species are poorly known; however, differences in food and reproductive resource use may represent an important form of partitioning among *Nicrophorus* and would be worth further investigation. The habitat associations of some *Nicrophorus* species may even be explained by differences in resource preferences, if their preferred resources are restricted to specific habitats.

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*, *Nicrophorus maculifrons* Kraatz, 1877, *Nicrophorus interruptus* Stephens, 1830, *Nicrophorus sepultor* Charpentier, 1825, and *Nicrophorus quadripunctatus* Kraatz, 1877, the North American species *Nicrophorus guttula* Motschulsky, 1845, and the Central American species *Nicrophorus mexicanus* Matthews, 1888 (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 *Nicrophorus investigator* Zetterstedt, 1824 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 *Nicrophorus tenuipes* Lewis, 1887 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). Likewise, the broadly distributed Palearctic species *Nicrophorus humator* (Gleditsch, 1767) may share a preference for coniferous forest with *N. defodiens* (Růžička 1994; Scott 1998; Urbański and Baraniak 2015; Çiftçi et al. 2018). Throughout their distribution in northern Europe and East Asia, *Nicrophorus vespillo* (Linnaeus, 1758) are predominantly associated with open fields, similar to *N. marginatus* (Scott 1998; Dekeirsschieter et al. 2011; Urbański and Baraniak 2015;

Çiftçi et al. 2018), but have also been found to be abundant in marshland (Růžička 1994), like *N. hebes*. Open-field specialists like *N. marginatus* appear to be common in other assemblages. Species such as *Nicrophorus antennatus* (Reitter, 1884), *Nicrophorus germanicus* (Linnaeus, 1758), and *Nicrophorus vestigator* Herschel, 1807 in Europe and Asia, and *Nicrophorus hybridus* Hatch and Angell, 1925, *Nicrophorus obscurus* Kirby, 1837, and *Nicrophorus carolinus* (Linnaeus, 1771) 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; Dekeirsschietter et al. 2011; Urbański 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.

## Conclusions

Co-occurring species of burying beetles are thought to partition resources to avoid interspecific competition and achieve stable coexistence. Here, we find evidence that some 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 three *Nicrophorus* species exhibit generalist habitat associations and overlap highly in habitat use with other co-occurring species. The habitat-generalist *Nicrophorus* species are instead thought to partition resources through seasonal differences in reproductive timing (Wettlaufer 2019). These 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 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 the processes that ultimately shape local diversity.

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## Supplementary material

### Variables measured in our study and description of the ground-level and canopy-level baited pitfall traps

**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.

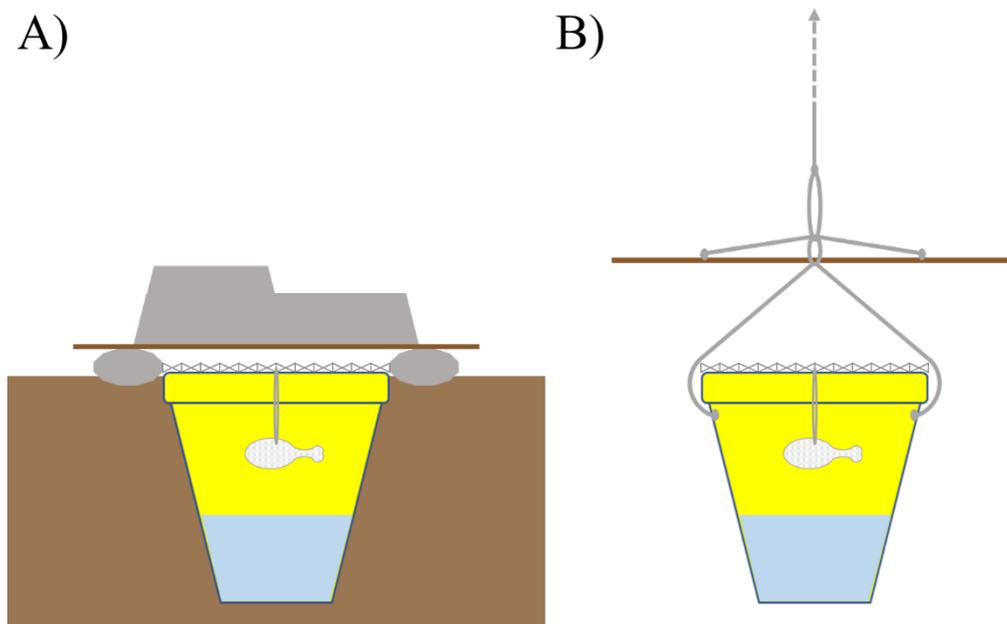
Variable	Abbreviation	Description
Trap type	“Trap”	Ground-level or canopy-level lethal pitfall trap; canopy traps were suspended 6 m above the ground and were paired with a ground-level trap at each site
Habitat type	“Habitat”	The type of habitat at each site, based on the dominant vegetation and substrate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

Percent ground covered by marsh vegetation	“Marsh”	The percentage of ground in our 2.5 m radius plots covered by marsh vegetation
Percent ground covered by open water	“Water”	The percentage of ground in our 2.5 m radius plots covered by open water
Percent ground covered by fallen logs	“Log”	The percentage of ground in our 2.5 m radius plots covered by fallen logs
Number of sugar maples ( <i>Acer saccharum</i> )	“Sugar.Maple”	The number of sugar maples with diameter at breast height (DBH) greater than 9 cm counted within our 17.25 m radius plots
Number of white ashes ( <i>Fraxinus americana</i> )	“White.Ash”	The number of white ashes with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of white birches ( <i>Betula papyrifera</i> )	“White.Birch”	The number of white birches with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of American beeches ( <i>Fagus grandifolia</i> )	“American.Beech”	The number of American beeches with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of eastern white pines ( <i>Pinus strobus</i> )	“White.Pine”	The number of eastern white pines with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of red juniper ( <i>Juniperus virginiana</i> )	“Red.Cedar”	The number of red junipers with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of red maples ( <i>Acer rubrum</i> )	“Red.Maple”	The number of red maples with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of green ashes ( <i>Fraxinus pennsylvanica</i> )	“Green.Ash”	The number of green ashes with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of basswoods ( <i>Tilia americana</i> )	“Basswood”	The number of basswoods with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of red oaks ( <i>Quercus rubra</i> )	“Red.Oak”	The number of red oaks with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of ironwoods ( <i>Ostrya virginiana</i> )	“Ironwood”	The number of ironwoods with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of white elms ( <i>Ulmus americana</i> )	“White.Elm”	The number of white elms with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of dead trees	“Dead”	The number of dead trees with DBH greater than 9 cm counted within our 17.25 m radius plots

Number of red pines ( <i>Pinus resinosa</i> )	“Red.Pine”	The number of red pines with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of silver maples ( <i>Acer saccharinum</i> )	“Silver.Maple”	The number of silver maples with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of white oaks ( <i>Quercus alba</i> )	“White.Oak”	The number of white oaks with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of trembling aspens ( <i>Populus tremuloides</i> )	“Trembling.Aspen”	The number of trembling aspens with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of bigtooth aspens ( <i>Populus grandidentata</i> )	“Bigtooth.Aspen”	The number of bigtooth aspens with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of blue beeches ( <i>Carpinus caroliniana</i> )	“Blue.Beech”	The number of blue beeches with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of eastern white cedar ( <i>Thuja occidentalis</i> )	“Nothern.White.Cedar”	The number of eastern white cedars with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of eastern hemlocks ( <i>Tsuga canadensis</i> )	“Eastern.Hemlock”	The number of eastern hemlocks with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of black cherry trees ( <i>Prunus serotina</i> )	“Black.Cherry”	The number of black cherry trees with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of shagbark hickory trees ( <i>Carya ovata</i> )	“Shagbark.Hickory”	The number of shagbark hickory trees with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of crab apple trees (genus <i>Malus</i> )	“Crab.Apple”	The number of crab apple trees with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of rock elms ( <i>Ulmus thomasi</i> )	“Rock.Elm”	The number of rock elms with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of white spruces ( <i>Picea glauca</i> )	“White.Spruce”	The number of white spruces with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of black ashes ( <i>Fraxinus nigra</i> )	“Black.Ash”	The number of black ashes with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of yellow birches ( <i>Betula alleghaniensis</i> )	“Yellow.Birch”	The number of yellow birches with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of common buckthorns ( <i>Rhamnus cathartica</i> )	“Common.Buckthorn”	The number of common buckthorns with DBH greater than 9 cm counted within our 17.25 m radius plots

Number of pear hawthorns ( <i>Crataegus calpodendron</i> )	“Pear.Hawthorn”	The number of pear hawthorns with DBH greater than 9 cm counted within our 17.25 m radius plots
Number of slippery elms ( <i>Ulmus rubra</i> )	“Slippery.Elm”	The number of slippery elms counted within our 17.25 m radius plots
Total number of tree species	“Total.Tree.Species”	The total number of tree species identified with DBH greater than 9 cm within our 17.25 m radius plots
Total number of trees	“Total.Trees”	The total number of trees with DBH greater than 9 cm counted within our 17.25 m radius plots
Total number of small trees	“Small.Trees”	The total number of trees with DBH between 9 and 23 cm counted within our 17.25 m radius plots
Total number of medium trees	“Medium.Trees”	The total number of trees with DBH between 23 and 38 cm counted within our 17.25 m radius plots
Total number of large trees	“Large.Trees”	The total number of trees with DBH greater than 38 cm counted within our 17.25 m radius plots

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**Fig. S1.** Diagrams of the (A) ground-level and (B) canopy-level baited pitfall traps used to collect carrion beetles in our 2017 survey of carrion beetle abundance and occurrence (for full details on trap construction see Wettlaufer et al. 2018). Ground traps were buried underground to their rim, whereas canopy traps were suspended 6 m above the ground using rope tied to an overhanging tree branch. Traps consisted of yellow plastic buckets 35 cm deep and 17 cm wide filled to approximately 15 cm with saturated saline water and baited with chicken wings wrapped in cheesecloth. Prior to deployment, the chicken wings were kept frozen without thawing or ripening. The chicken wings were suspended above the saline solution by wrapping a piece of steel craft wire around the chicken wing and attaching it to the center of a 35 cm<sup>2</sup> square of chicken wire placed over the opening of the bucket. To prevent rainfall from entering the bucket, each trap was covered with a 30 cm<sup>2</sup> plywood board elevated slightly above the bucket's lip. For canopy traps, the board was suspended above the opening of the bucket by looping a rope handle from the sides of bottom through a small hole in the board. A second rope handle attached to the board was then fed through a small loop of the bucket's handle extending through the hole in the board and connected to longer rope used to hoist the trap into the forest canopy. For ground traps, large stones were placed on top of the board to deter vertebrate scavengers from disturbing the traps.

## Habitat use of Silphinae in southeastern Ontario

Four other carrion beetle species co-occur with the genus *Nicrophorus* in southeastern Ontario: *Necrophila americana*, *Oiceoptoma inaequale*, *Oiceoptoma noveboracense*, and *Necrodes surinamensis* (subfamily Silphinae). These species also feed and reproduce on carrion; however, unlike *Nicrophorus*, they do not bury carcasses, nor 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. *Necrophila americana* have been found in forests, open fields, and wetlands, but they are often most abundant in forest or wetland habitats (Anderson 1982; Shubeck 1983; Anderson and Peck 1985; Lingafelter 1995; Ratcliffe 1996). *Oiceoptoma 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 been captured less commonly in open areas and marshes (Anderson 1982). *Necrodes surinamensis* are relatively rare compared with 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).

During our survey of burying beetle abundance and occurrence on the properties of the Queen's University Biological Station (refer to the Materials and methods of the main text), we also collected a total of 3547 beetles belonging to the four Silphinae species (Table S2). As with *Nicrophorus*, we examined 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 by generating conditional inference trees using the function “ctree” from the R package “partykit” version 1.2-2 (Hothorn et al. 2006; Hothorn and Zeileis 2015). In our conditional inference trees, we used the mean abundance of each species in ground and canopy traps at each site as the response variable, and trap type (ground or canopy) and all 54 measured habitat characteristics as the predictor variables.

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 Silphinae species (*Necrophila americana*, *O. inaequale*, and

*O. noveboracense*). However, we were unable to identify the habitat associations of *Necrodes surinamensis*. Most *Necrophila americana* were caught in ground-level traps ( $n = 100$  traps, Fig. S2A;  $n = 100$ , Fig. S2B). *Oiceoptoma inaequale* were most abundant ( $n = 100$  traps; Fig. S2C) and commonly caught in ground-level traps ( $n = 100$  traps; Fig. S2D), but they were also found in some canopy-level traps at sites with many red oaks ( $n = 15$  traps). Likewise, *O. noveboracense* were most abundant ( $n = 100$  traps; Fig. S2E) and most likely to be present ( $n = 100$  traps; Fig. S2F) in ground-level traps. *Necrodes surinamensis* were not associated with any habitat characteristics and were rare or absent in most traps ( $n = 199$  traps; Figs. S3A and S3B).

Three of the Silphinae carrion beetle species included in our analyses were 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). We found *Necrophila americana* to occur abundantly in ground-level traps in all habitat types (Figs. S2A and S2B). *Necrophila americana* may be unrestricted in their habitat use due to their ability to use carcasses of all sizes and the lack of significant competition from *Nicrophorus*, which prefer small carrion, and other Silphinae, which are generally smaller and less abundant (Table 1; Anderson and Peck 1985; Ratcliffe 1996; Collard 2018). We found *O. inaequale* and *O. noveboracense* were also most abundant and common in ground-level traps, regardless of surrounding habitat features (Figs. S2C–S2F), but *O. inaequale* also occurred in some canopy-level traps at sites with many red oaks, hinting at a possible preference for forest habitat with trees attractive to small vertebrates. It is possible that *O. noveboracense* may have a similar preference for forest habitats but are excluded from them at our study site by the more abundant *O. inaequale*.

We were unable to identify the habitat associations of *Necrodes surinamensis*. This species was rare or absent in most traps, regardless of the surrounding environment (Figs. S3A and S3B). During our sampling period, we collected only 34 *Necrodes surinamensis* at 14 different sites with varying habitat characteristics, which may have limited our ability to identify their habitat associations (Table S2). The chicken wings that we used to bait our traps may have been insufficient to attract *Necrodes surinamensis* in large numbers, as adult *Necrodes surinamensis* tend to seek out large carrion such as deer for reproduction and feed primarily on

fly maggots (Ratcliffe 1972; Anderson 1982; Anderson and Peck 1985). Other carrion beetle surveys have also found *Necrodes surinamensis* to be uncommon in the region (Anderson 1982; Robertson 1992).

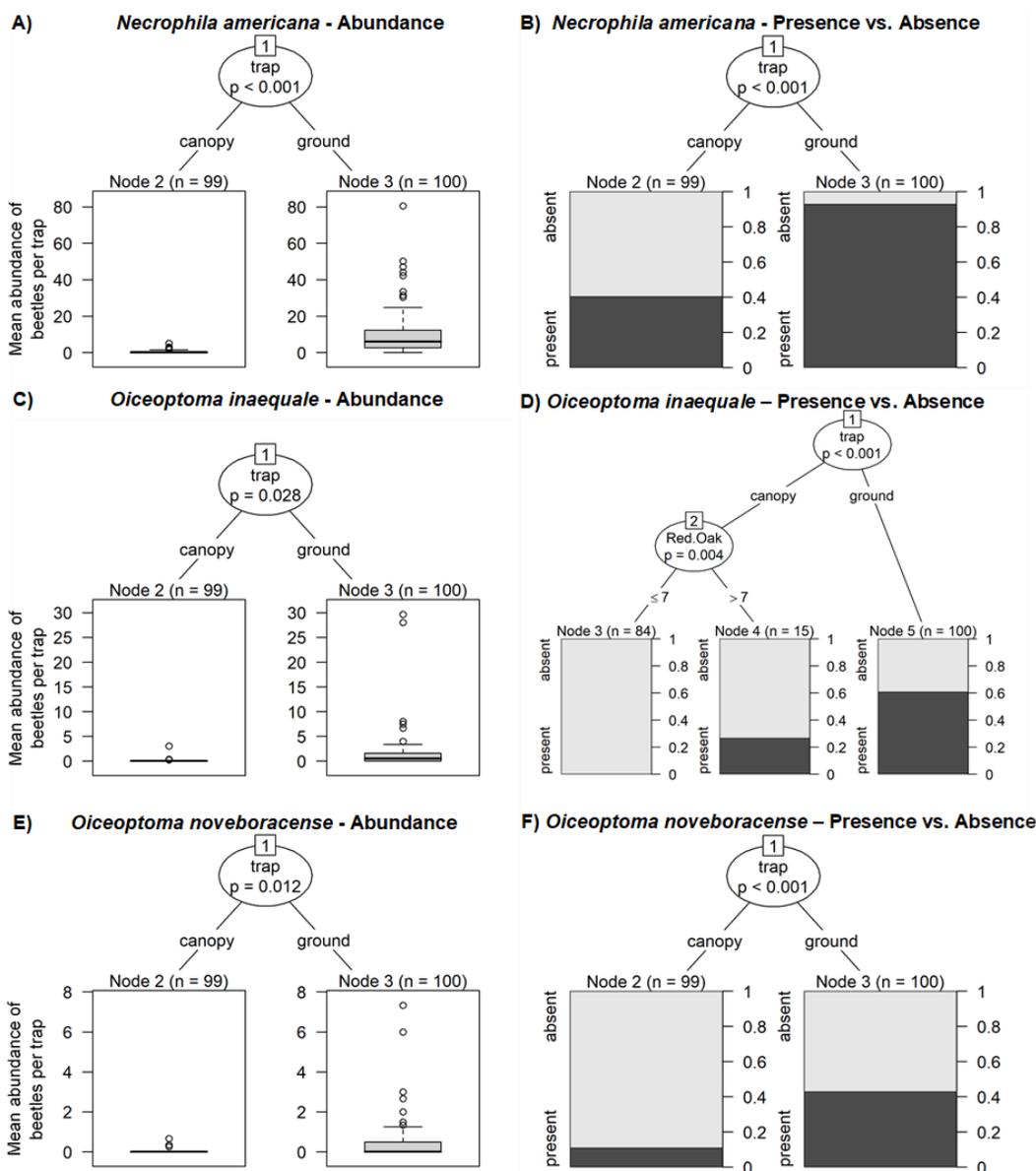
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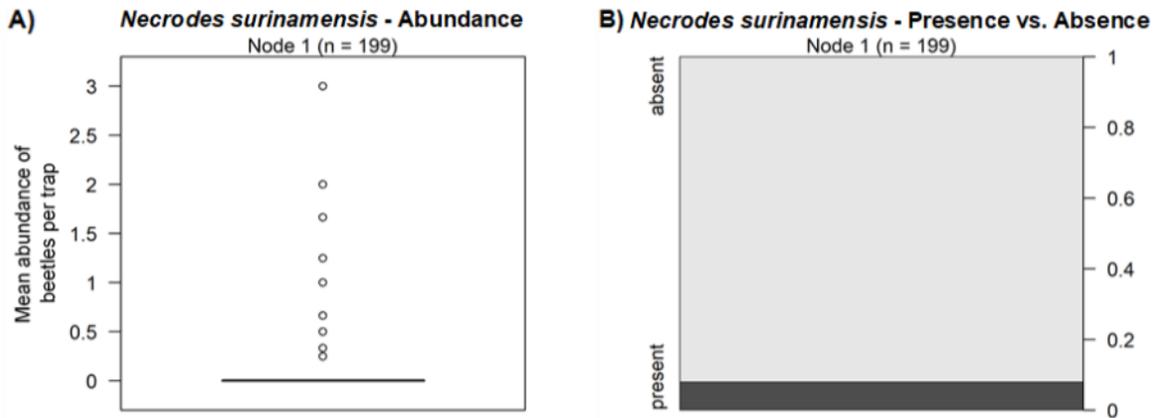
**Table S2.** Counts of carrion beetles belonging to the subfamily Silphinae collected in ground-level and canopy-level traps between April and October 2017 during our survey of carrion beetle species abundance on the properties of the Queen’s University Biological Station.

Silphinae species	Ground-level traps		Canopy-level traps		Total	
	Number of individuals	Number of traps	Number of individuals	Number of traps	Number of individuals	Number of traps
<i>Necrophila americana</i>	2824	161	156	44	2980	205
<i>Oiceoptoma inaequale</i>	390	79	12	4	402	83
<i>Oiceoptoma noveboracense</i>	119	50	12	11	131	61
<i>Necrodes surinamensis</i>	17	11	17	5	34	16
Total	3350	277	197	327	3547	604



**Fig. S2.** Conditional inference trees displaying significant associations between local habitat characteristics and 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. The  $n$  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) *Oiceoptoma inaequale* were present (dark shading) in a greater number of ground-level traps, but they were also present in some canopy-level traps at sites with many red oaks.

(E) *Oiceoptoma noveboracense* mean abundance and (F) occurrence were greater in ground-level traps.



**Fig. S3.** Conditional inference trees displaying significant associations between local habitat characteristics and (A) *Necrodes surinamensis* mean abundance and (B) *Necrodes surinamensis* occurrence. Boxplots show the medians, ranges, and upper and lower quartiles of mean abundance in the final groupings produced after splitting. The  $n$  values indicate the number of traps (ground and canopy) included in each node. No significant associations were identified between any habitat variables and mean abundance or occurrences of *Necrodes surinamensis*.