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Substantial niche overlap in carrion beetle habitat and vegetation use

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Abstract

1. The habitat affinities of carrion beetles (Coleoptera: Silphidae), a speciose group with wide cooccurrence, are only coarsely described for well-studied species, particularly in the western United States.
2. We aim to identify if the 15 species of montane carrion beetle in Colorado differ substantially in their use of habitats and across more uniquely defined, fine-scale vegetation characteristics.
3. Habitat and vegetation data as well as carrion beetle abundance were collected along four elevational transects in the Front Range and San Juan Mountains from 2010 to 2012 across 32 sites. Multiple habitat types were sampled, including forest, meadow, riparian, rocky outcrops and tundra. The fine-scale vegetation characteristics included percent coverage of ground vegetation (grass, forb, shrub, cacti, bare ground), understory vegetation biomass and height, canopy cover and tree species, number and size. Canonical correspondence analysis models examined whether vegetation characteristics strongly segregated species using abundances and presence-absences.
4. Habitat and vegetation models explained a maximum of 18.93% of the variation in species' abundances and 2.48% in species' presence–absences. Only one likely habitat specialist was identified by the models (*Heterosilpha ramosa*) and the remaining species had substantial overlap in habitat and vegetation use. The arid, low productivity and generally open understory habitats in Colorado mountains likely play a large role in the substantial vegetation overlap.
5. Other mechanisms of partitioning likely exist in this system to reduce niche overlap, which could include differences in activity time and seasonality, physiological traits, other life history strategies and body size.

KEYWORDS
beetle, coexistence, habitat, partitioning, Silphidae, vegetation

INTRODUCTION

Ecological specialisation has been the focus of empirical research in community ecology for decades because of its relevance to species' vulnerability to human disturbance and global climate change (Futuyma & Moreno, 1988, Hille Ris Lambers et al., 2012, Mimet et al., 2019). Habitat specialisation is particularly important given the widespread modification of landscapes and the interacting abiotic and biotic effects of rising temperatures (Parmesan 2006, Gilbert et al., 2008, Kadlec et al., 2009). With the more recent focus on the importance of the microclimate, the scale at which habitat specialisation is examined has become smaller because of the effect vegetation has on temperatures within an environment (D'Odorico et al., 2013; Pincebourde & Woods, 2020). Despite the important implications for conserving biodiversity, differences in fine-scale vegetation use across species in a community are often unknown.

The use of habitat by carrion beetles has been widely studied (Anderson, 1982, Estrada et al., 1998, Díaz, Galante & Favila 2010; Caballero & León-Cortés 2014, Engasser 2021, Fusco et al., 2017, Gao et al., 2017, Leasure, 2017, Wettlaufer et al., 2018). Carrion beetles are a unique family of insects (Coleoptera: Silphidae) that use vertebrate carrion as food and reproductive resources (Scott, 1998). There are two subfamilies of carrion beetle, the smaller Silphinae which reproduce on large carrion and the larger Nicrophorinae which reproduce on small carrion they bury to provision for their offspring. In Colorado, 15 species of carrion beetles have been detected between 1400 and 3700 m above sea level, and most species have largely overlapping elevational ranges (McCain, 2021). The considerable overlap in carrion beetle ranges is surprising considering all of these beetles are specialists on the same types of food and reproductive resources (Peck, 2001; Peck & Kaulbars, 1987). Even though carrion beetles compete to discover carcasses quickly before other carrion beetles can challenge them and possibly rob them of carcasses, there is little evidence that large-scale trends in carrion beetle abundance in Colorado are limited by mammal resources (McCain, 2021). Given the large number of species that cooccur, it is likely that species differ in their use of habitat (Lawton & Strong, 1981; Peck & Beninger, 1992). Previous analyses of carrion beetles in mountain systems in Colorado detected a strong positive relationship of carrion beetle diversity with understory plant biomass during the growing season (McCain, 2021), but it has yet to be tested how habitat and vegetation associations differ across subfamilies and by species.

While carrion beetles are thought to differ in activity time, seasonality and physiology, there is evidence that they also differ substantially in vegetation usage (Anderson & Peck, 1985). Research on carrion beetle vegetation usage, which has primarily utilised coarse-scale vegetation assessments and broad habitat types, has found differences in habitat associations among some carrion beetle species (Anderson, 1982, Estrada et al., 1998, Díaz et al. 2009; Jakubec & Růžička, 2012; Caballero & León-Cortés 2014, Engasser 2021, Leasure, 2017). Some species in the northeastern US like *Nicrophorus pustulatus* (Herschel) and *Nicrophorus investigator* (Zetterstedt) are found in all habitat types, while others like *Nicrophorus americanus* (Olivier) are considered specialists on field habitats (Scott, 1998). However, habitat associations often conflict and differ by region; for example, in Arkansas, high *N. americanus* abundance is associated with grasslands as well as open-canopy woodlands (Leasure, 2017). More specific associations, such as greater abundances in the canopy than on the ground (*N. pustulatus* in Canada) or preferences for burying carcasses in sunny rather than shaded areas (*N. investigator* in Colorado), are known only for the few well-studied species (Wettlaufer et al., 2018, Burke et al., 2020, Smith & Heese, 1995). Information on habitat associations is limited in terms of detail and specificity as well as spatial and temporal extent. While broad habitat associations are known for some species in the United States, habitat associations for species in Colorado and links to specific vegetation traits are largely unknown. This study uses fine-scale vegetation measurements to identify which habitat and vegetation characteristics, including elevation, canopy cover, understory vegetation height, plot coverage of grass, forbs, shrubs, cacti and bare ground, and species, number and size of trees, within a habitat are used preferentially by each carrion beetle species.

Preferences for specific vegetation components could be motivated by food, reproductive, thermal, or predator-avoidance needs. Understory vegetation like grass and forbs could restrict carrion beetle movement, especially when transporting carcasses (Crist et al., 1992). Dense ground vegetation could also restrict reproductive behaviours of the Nicrophorinae during resource movement and burial. For two species of Nicrophorinae that cover burial chambers with vegetation debris rather than soil, plant litter accumulating in or under in vegetation could provide coverage material (Anderson & Peck, 1985; Scott, 1998). Leaf litter and larger vegetation like shrubs and trees could also provide distinct microclimates (Parmenter et al., 1989). Alternatively, mammals themselves may have preferences for certain types of vegetation microclimates due to their climatic, food, or predator-avoidance preferences, which influence carrion beetle usage (Simonetti, 1989).

The goal of this study was to determine if carrion beetles in the Southern Rocky Mountains have strong vegetation affinities. Fine-scale vegetation attributes might be differentially important to carrion beetle species; thus, we predicted that the vegetation attributes associated with the presence or increased abundance of each beetle species would differ. To test for evidence of specialisation, we compared associations among habitat types, vegetation measurements and elevation with carrion beetle abundances and presence–absence data.

MATERIALS AND METHODS

Sites and plots

Sites were established along four elevational transects in the Colorado Rocky Mountains over 3 years (2010–2012; Figure 1a; McCain, 2021). Two transects were established in the San Juan Mountains in southwestern Colorado and two were established in the Front Range Mountains in northcentral Colorado. The sampling was designed to provide replicate transects and capture the variation in climate and habitat in the Colorado Rocky Mountains, which are predominantly arid, low in productivity and highly variable locally. Generally, the more southwestern San Juan Mountains are warmer but less arid at the higher elevations than the Front Range Mountains. While both receive substantial snow in the winter, the San Juans receive more high-elevation summer precipitation, while desert habitats dominate at low elevations. These two mountain ranges and our sites also have a variety of habitat types ranging from desert and arid grasslands to various forest types and finally high-elevation tundra.

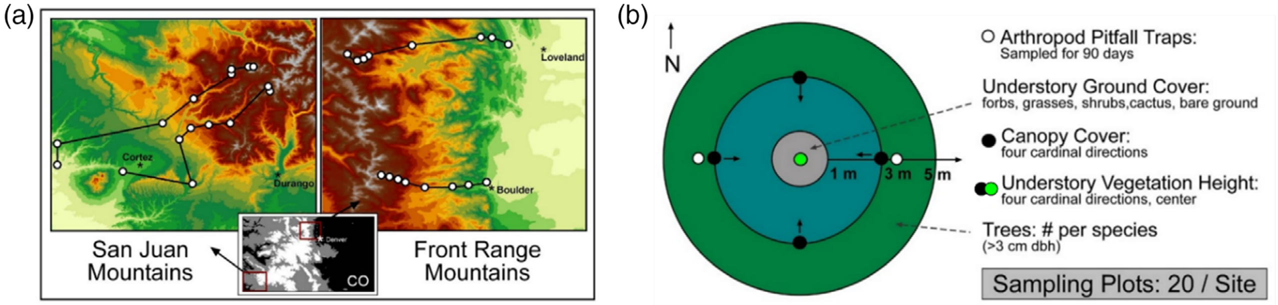

FIGURE 1 (a) The four elevational transects in the Colorado Rocky Mountains: two in the southwestern San Juan Mountains and two in the northeastern Front Range Mountains. Each transect includes eight sites (white circles) spread between the base and top of the mountains. Coloration indicates elevation from light green at low elevation to red and grey at the highest elevations. The black and white inset is the entire state of Colorado (CO, USA) for scale. (b) Sampling plots for vegetation and arthropods. Various vegetation measurements were conducted within the 1, 3, and 5 m radius circles, including Braun-Blanquet coverages of understory (<1 m height) vegetation classes. Understory vegetation height and canopy cover were surveyed at the edges in four cardinal directions along the 3 m radius (black circles). Pitfall traps (white circles) were placed near the E and W 3 m points. Sampling plots were placed along transects through all habitats at a site (e.g., forest, riparian, meadow).

Transects extended from the base of the mountains to the upper limit of vegetation on the mountain tops. Each of the four transects had eight sites located every 200–300 m in elevation for a total of 32 sites. Within each site, 20 standardised sampling plots were established along a transect created to intersect with major habitat types across the site. The sampling plots were located every 70 m along those transects and consisted of concentric circles of 1, 3 and 5 m (Figure 1b). As vegetation measurements at the plot-level are at a finer scale than site-level averages, plot-level vegetation measurements and habitat characteristics are used in this analysis with the paired pitfall trap data for carrion beetles.

Vegetation assessments

The vegetation measurements taken in the field included understory vegetation coverage, height of vegetation, canopy coverage, abundance and DBH (diameter at breast height) of each tree species, and any notes on general characteristics unique to each plot. Vegetation was assessed in each plot three times over a growing season: early summer, mid-summer and late summer. In each plot's 1-m circle, Bran-Blanquet coverage classes (Barbour et al., 1999; Cain & de Oliveira Castro, 1959) were estimated for groundcover less than 1 m in height including bare ground and grasses, forbs, shrubs and cacti. Coverages were estimated simultaneously by two observers who conferred before data were recorded. Coverages were recorded as scores between 0 and 5 (0 = 0–1%; 1 = 1–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 > 75%) which were later converted into percentage midpoints (score of 1 = 2.5%; 2 = 15%; 3 = 37.5%; 4 = 62.5%; 5 = 87.5%). The percentage midpoints were averaged across the three seasonal measurements to produce average coverages for grass, forbs, shrubs, cactus and bare ground at each plot. The height of this understory vegetation was measured within the 3-m circle at the centre and at the edges in the four cardinal directions with a yardstick. For sites with bare ground around the measurement locations, the height of the tallest vegetation within one hand's breadth was recorded or if none was present, vegetation height was recorded as zero. Vegetation heights were averaged among the five measurements and then across the three seasonal measurements for average vegetation heights at each plot. To calculate average understory plant biomass at each plot, the percentage of forb, grass, shrub and cactus coverage across the summer were averaged and multiplied by the average vegetation height (Cheippa et al., 2020). To calculate the sum of plant biomass at each plot, the percentage of forb, grass and shrub coverage was summed across the summer and multiplied by the average vegetation height. Canopy cover was measured with a spherical concave densitometer at the edges of the 3-m circle in the four cardinal directions while facing the centre point of the plot. Percent canopy covers were estimated and averaged across the three measurement timepoints for canopy covers at each plot. Trees with a DBH greater than 3 cm were identified, counted and measured at 1.5 m in height for all observers for DBH in cm within the 5-m circle at each plot.

Arthropod sampling

Arthropod sampling was conducted using pitfall traps. Two pitfall traps were set at each of the 20 plots, at the eastern and western edges of the 3 m circle, for a total of 40 traps per site. Traps consisted of two nested 16-ounce cups buried so the lips were flush with the ground, covered with a small plate held 3–5 cm above the cups to protect from rainfall, and filled to one-third full with a propylene glycol preservative (Brown & Matthews, 2016). Three 30-cm-long wooden shims were fanned out around the cups to increase the ground surface-area where insects would be intercepted and directed towards the pitfall trap. Pitfall traps were in place for a total of 90 days at each plot and were collected and reset a variable number of times over the summer with the sampling duration for each collection being recorded. Particularly at high elevation sites, there was mammal disturbance (i.e., bears, marmots) of pitfall traps leading to fewer traps nights at some sites. Carrion beetles collected during this 90-day period were cleaned, identified to species, counted and preserved. For this analysis, the abundances from the east and west pitfall traps were combined for an overall plot-level abundance matching the scale of the vegetation data.

This project was originally designed to assess the arthropod biomass available as mammal food resources as well as assess small mammal diversity and abundance, and carrion beetles were abundant and widespread in these pitfalls. As carrion beetles were not the initial target taxa, pitfalls were unbaited and did not contain any carrion beetle food or attractants except unstandardised shrew, rodent and other vertebrate bycatch. Pitfall traps for carrion beetle collections are typically baited, attracting feeding and breeding individuals from over to a mile away (Jurzenski et al., 2011). The unbaited pitfalls used here provide a more unbiased picture of carrion beetle movement and behaviour by passively collect carrion beetles that are actively using the habitat during feeding, breeding and interacting with other species. Unlike baited pitfalls, unbaited pitfalls also have the ability to survey carrion beetles during behavioural thermoregulation, predator avoidance and even resource movement and burial. We have conducted both baited and non-baited trapping in a subset of these sites and both methods result in similar collections across habitats and vegetation (Appendix S2, Figures S1, S2). We have used only collections from the unbaited pitfalls in the analysis because only these trapping locations have the associated high-quality vegetation data. While the majority of carrion beetles were collected in pitfalls without vertebrate bycatch, some pitfalls were unintentionally baited by collections of shrews, voles and mice ($n = 872$ vertebrates at sites with Silphid captures), which were also preserved in the propylene glycol. Despite this sporadic, unintentional baiting, the abundance and distribution of carrion beetles were not associated with the distribution of these preserved vertebrate specimens across pitfalls (McCain, 2021). Nonetheless, there is some influence of feeding behaviour embedded within our pitfall collections.

Data analysis

Canonical correspondence analysis (CCA) was used to assess the relationship between environmental variables and the presence or abundance of each species (ter Braak & Verdonschot, 1995). Carrion beetle abundances as well as separate analyses for presence–absence data from each pitfall were used in the CCA as this method has been shown to perform well with pitfall trap abundance data and skewed species' distributions (McIntyre et al., 2000; Palmer, 1993). A direct gradient analysis method, in which ordination axes are constrained by environmental variables, was chosen so variation in the presence or abundances could be directly related to variation in habitat and vegetation characteristics (ter Braak, 1987). To assess the influence of species with relatively low total abundances across all sites and collection periods or species found to be present at few sites, analyses were performed both with and without the inclusion of these relatively rare species. Relatively rare species were defined here as species present at only a single site. Three relatively rare species were identified (Table 1, starred): *Thanatophilus coloradensis* (Wickham), *Nicrophorus obscurus* (Kirby) and *Nicrophorus carolina* (Linnaeus). One of these rare species, *T. coloradensis*, is a high-elevation specialist with a range limited to above the treeline (Peck & Anderson, 1982).

Variables used in the CCA from each sampling plot included habitat type, elevation, the average, maximum and minimum ground coverage of bare ground, forbs, grasses, shrubs and cacti per site, the number of trees, average DBH, tree species identity, average canopy cover, average vegetation height, average plant biomass and sum plant biomass. Variables were numerical except habitat type and tree species, which were coded in the form of dummy variables with each category being assigned an integer (Hejcmanova-Nežerková & Hejcman, 2006). To account for differences in scale of the numerical environmental variables, these variables were *z*-score transformed by subtracting the mean from each value and dividing by the standard deviation (Ramette, 2007; Xu et al., 2008).

Initial variable selection followed procedures for forward selection using permutation tests as outlined in ter Braak and Verdonschot (1995). All variables significant at the $\alpha = 0.05$ level when included as the only variable explaining presences or abundances were added to the models. In the case of variables that encompassed other variables, such as average plant biomass and sum plant biomass, which are calculated from vegetation height and coverages, model selection was completed for each set of variables separately if both sets of variables were significant. To avoid overfitting and ensure that weights were stable enough for interpretation, the number of variables in the model was then reduced (ter Braak, 1987, Dixit et al. 2001). Criteria for removal included variables that were weakly correlated with the first and second axes ($r < |0.5|$) and that when removed from the model, resulted in less than a 2% decrease in the variation explained by the first and second axes (Xu et al., 2008). When two highly correlated ($r > |0.7|$) variables were present in the same model, the variables were compared using the same criteria and the variable less correlated with axes and explaining less variation was removed. Moderately correlated variables were not removed as CCA is robust to moderate collinearity (Palmer, 1993). Variance inflation factors (VIFs), which quantify the increase in standard error for each variable relative to what the standard errors would be if there was no collinearity between model variables, were also assessed. Variables with VIFs larger than 5 were removed from the models (Xu et al., 2008). CCA and model selection were performed in R 3.6.2 using v2.5–6 of the package vegan (R Core Team 2014, Oksanen et al., 2019).

RESULTS

Between 2010 and 2012, a total of 3566 carrion beetles were collected; 2182 in the Front Range transects and 1384 in the San Juans transects. A total of 14 unique species were collected. In the Front Range, 13 different species were collected, with a maximum of 11 species being found at any one site, while in the San Juans, six species

TABLE 1 For each species, in order of overall abundance, the total number of carrion beetles collected from all locations over all dates and the number of plots and sites of collection are listed. Also included are the minimum and maximum collection elevations for each species.

Species	Number collected	Number of plots	Number of sites	Minimum elevation (m)	Maximum elevation (m)
Heterosilpha ramosa (Say)	1674	23	8	1479	2650
Nicrophorus tomentosus (Weber)	752	40	7	1718	2410
Thanatophilus lapponicus (Herbst)	425	41	5	1723	3638
Nicrophorus guttula (Motschulsky)	271	19	8	1481	2363
Nicrophorus marginatus (Fabricius)	105	14	6	1726	2242
Nicrophorus hybridus (Hatch, Angell)	90	10	4	1723	2181
Nicrophorus mexicanus (Matthews)	81	23	9	1718	2406
Nicrophorus investigator (Zetterstedt)	75	19	10	1885	3269
Nicrophorus defodiens (Mannerheim)	52	19	5	1793	3020
Oiceoptoma noveboracense (Forster)	20	5	3	1718	2168
*Thanatophilus coloradensis** (Wickham)	17	1	1	3638	—
*Nicrophorus obscurus** (Kirby)	3	3	1	1723	1734
*Nicrophorus carolina** (Linnaeus)	1	1	1	2112	—

Note: Species that are defined here as relatively rare as denoted with a star following the species name.

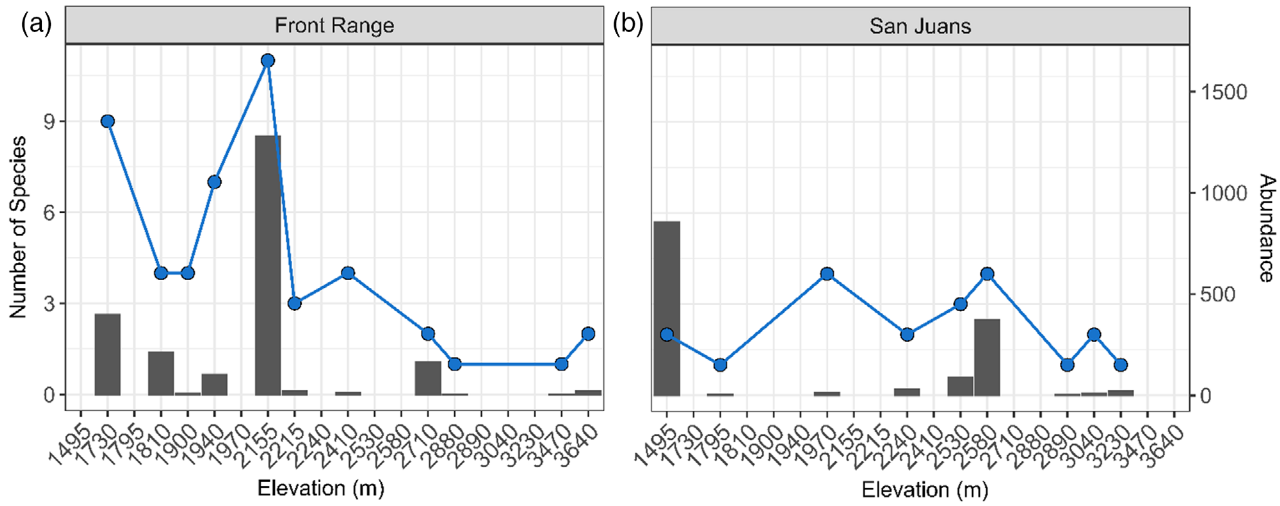

FIGURE 2 Carrion beetle species richness (blue lines) and abundance (grey bars) across elevation in each range. (a) Front Range Mountains and (b) San Juans Mountains include all data for the two transects in each range.

with maximum of four species at any one site were collected (Figure 2). Traps were relatively evenly spread across habitat types, with the exception of tundra habitats, which are only present above the treeline in this system (Figure S3). Vegetation measurements widely varied across mountain ranges, transects and sites. While vegetation coverages tended to be consistent across low and mid elevations with declines at high elevations, many summary measures such as vegetation height and biomass showed steadier declines with elevation (Figure S4). The number of trees tended to decrease with elevation, whereas the average canopy cover and average tree DBH (diameter at breast height) increased with elevation (Figure S4b, f).

Modelling

Canonical correspondence analysis (CCA) models were built to model both presences and abundances of both all species and only non-rare species. Within each of the four types of models (all species abundance, all species presence-absence, non-rare species abundance, non-rare species presence-absence), the model explaining the greatest percentage of variation in the data was considered the best model. In all cases, models explaining abundances across plots performed better than those explaining presences and absences, and models excluding rare species performed better than those including all species. The

TABLE 2 CCA results for the best model including standardised canonical coefficients (SCC, the components of a linear formula used to estimate sites scores based on environmental data at that site) and the intra-set correlations (ISC, correlations of environmental variables and axes) for the first axis.

Variable	*p*-value	SSC Axis 1	ISC Axis 1
Average of DBH	0.001	1.0618	0.5369
Presence of Riparian Habitat	0.001	−1.510	−0.5419
Maximum Vegetation Height	0.441	−0.0344	−0.5163
Maximum Percent Coverage of Grass	0.307	0.7278	−0.3312
Maximum Percent Coverage of Forbs	0.004	−0.2448	−0.2885

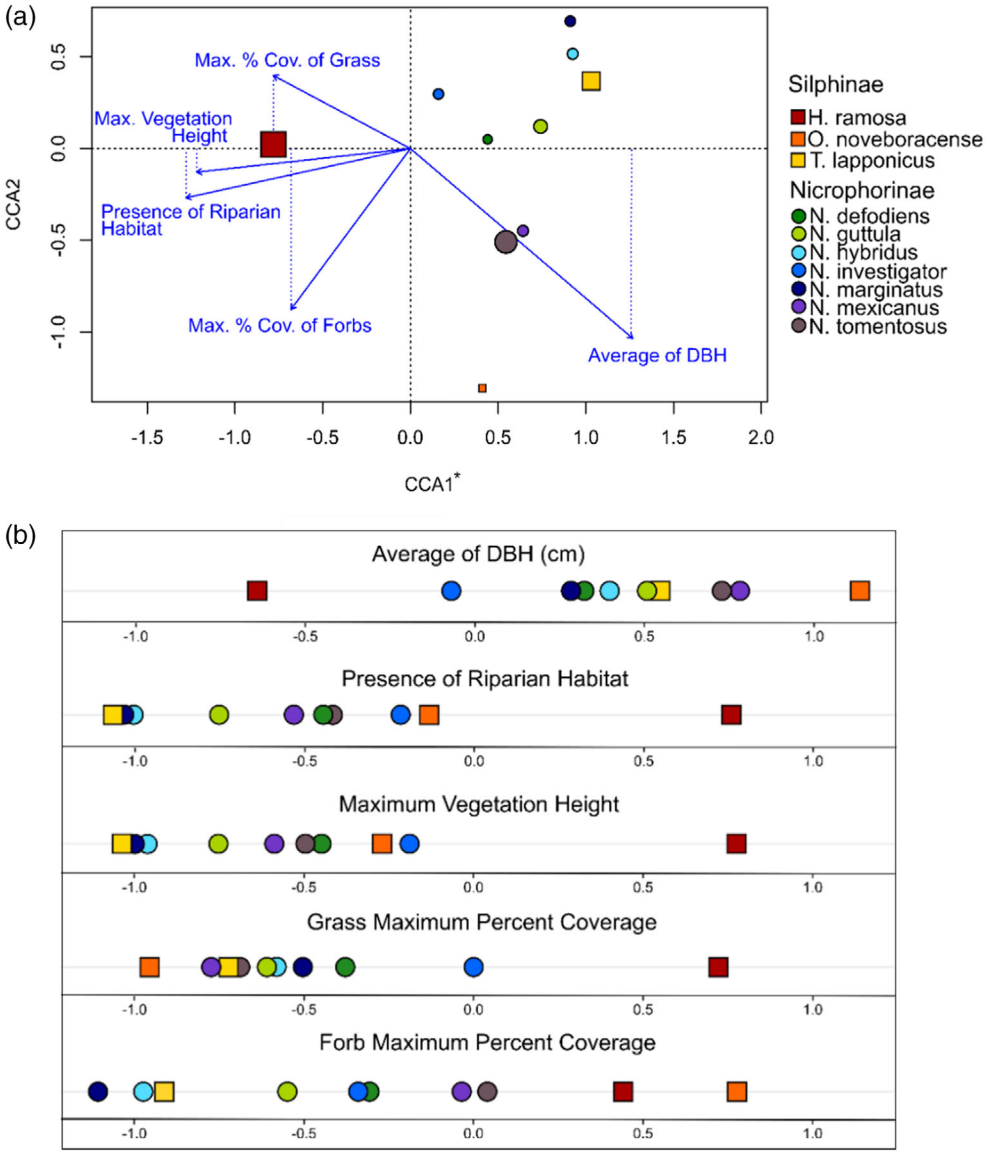

FIGURE 3 (a) CCA biplot of the best model showing the first (significant) and second (insignificant) CCA axes, the environmental axes in blue, and the position of each species (colour-coded points) in the ordination space. The size of each symbol indicating the position of a species in ordination space is scaled by abundance, with larger symbols representing more abundant species. Dashed blue lines connecting environmental axes points and the *x*-axis highlight that as only the first axis is significant, only the horizontal positions of each species show significant differentiation. (b) Number-line representations of the position of each species along the environmental axis of each variable included in the best model (see Appendix S1 for methods). As environmental axes are two dimensional, these points represent the position of each species relative to both axes, though importantly only the first axis was significant at a 0.05 level.

best model for presences and absences of all species included one variable, the presence of riparian habitat. This model was not significant ($p = 0.103$) and explained only 1.6% of the variation in the data. The best model for abundance of all species included average diameter at breast height (DBH) of trees, the maximum understory vegetation height, the presence of forest habitat and the presence of riparian habitat. This model was significant ($p = 0.001$) and explained 12.83% of the variation in the data. Neither of the models considering all species included elevation as a significant predictor, and neither model differentiated the high elevation specialist *Thanatophilus coloradensis* from other species based on other (non-elevation) variables. The best model explaining presences and absences of only non-rare species included three variables: the number of trees, the presence of riparian habitat and the average percent coverage of cacti. This model was also significant ($p = 0.001$), explaining 2.48% of the variation in the data. The overall best model was the model explaining abundance of only non-rare species across plots, which included the average of tree DBH, the presence of riparian habitat, the maximum vegetation height, the maximum percent coverage of grass and the maximum percent coverage of forbs. This model was significant ($p = 0.001$) and explained 18.93% of the variation in the data. Details on the overall best model are provided here with additional details on other models provided in Tables S1 and S2.

For the best model, both the first ordination axis and the overall model were significant (based on 1000 permutation tests, 1st CCA axis: $p = 0.001$, model: $p = 0.001$). As only the first CCA axis was significant, the model explained a total of 18.93% of the variation in the data. The eigenvalue of the first ordination axis, reflecting the amount of variation the axis accounts for, was 0.5783. The species-environment correlation for this axis, the correlation between the environmental axis and species scores along it, was 0.7877. Variables in the model were significant except for the maximum vegetation height and the maximum percent coverage of grass, which were included because each improved the model in accordance with model selection criteria (Table 2). The first CCA axis was moderately, positively correlated with the average of DBH (Table 2, $r = 0.54$). It was also moderately, negatively correlated with the presence of riparian habitat ($r = -0.54$) and the maximum vegetation height ($r = -0.5419$). Correlations between the first axis and the remaining variables were weak ($r < |0.5|$). This axis may reflect differences in habitat caused by the effect of tree cover and resulting shade on understory growth, as maximum vegetation height and average of DBH are partitioned on opposite ends of this axis. Similarly, axis correlations suggest that in riparian study sites, vegetation was taller and average DBH was lower. The second axis, which was close to a significance level of 0.05 but was not significant ($p = 0.087$), explained an additional 10.46% of the variation in the data. This second axis was positively correlated with the maximum percent coverage of grass, and negatively correlated with the remaining variables. The strongest correlations were the negative correlations between the second axis and the average DBH and the maximum percent coverage of forbs (Figure 3a).

The first CCA axis strongly differentiated the most abundant (but not most widespread) species *Heterosilpha ramosa* (Say) from other species (Figure 3). High abundances of *H. ramosa* were associated with smaller trees (lower DBH), taller understory vegetation (maximum vegetation height) and high ground coverages of grasses and forbs (maximum percent coverages). *H. ramosa* was also more abundant at riparian sites than all other species considered (Figure 4). There were no discernable patterns of differentiation for the remaining species when considering only the first CCA axis. While *H. ramosa* was at the extreme ends of all environmental axes, these differences translate to relatively small differences between actual vegetation values and habitat usage (Figures 4 and 5). The majority of species were collected across strikingly similar ranges of vegetation variables and in similar habitat types, with the exception of rare species that were collected in few locations and have more specific habitat and vegetation associations as a result. Overall, non-rare species were collected over the entire range of values for each measured vegetation characteristic, which reflects the high degree of overlap in species' vegetation use (Figure 5). When considering the first two axes together, although the second axis was insignificant, a slight differentiation of the species *Oiceptoma noveboracense* (Forster) was evident as the species was associated with larger trees and more forbs relative to other species. The first two axes from this model did not differentiate any of the other nine species.

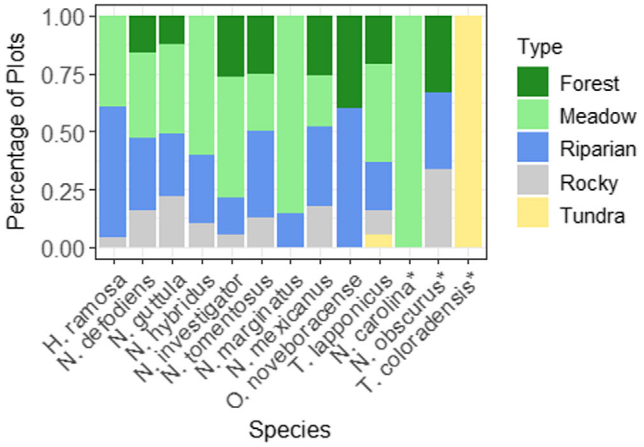

FIGURE 4 Distribution of habitat types that carrion beetles were collected is shown by species. All species and collections across all ranges, transects and sites are included. Rare species not included in the best model are denoted with a star and have been arranged on the right side of the figure. The three rare species are *N. carolina* ($n = 1$, 1 plot at 1 site), *N. obscurus* ($n = 3$, 3 plots at 1 site), and *T. coloradensis* ($n = 17$, 1 plot at 1 site).

Discussion

As a group with diversity and cooccurrence as the rule, beetles provide an ideal study system for investigating fine-scale specialisation within a habitat. Here, we focused on a relatively small group of understudied carrion beetle species with largely overlapping elevational ranges in the mountains of Colorado. Using a uniquely extensive set of vegetation attributes and carrion beetle abundance data

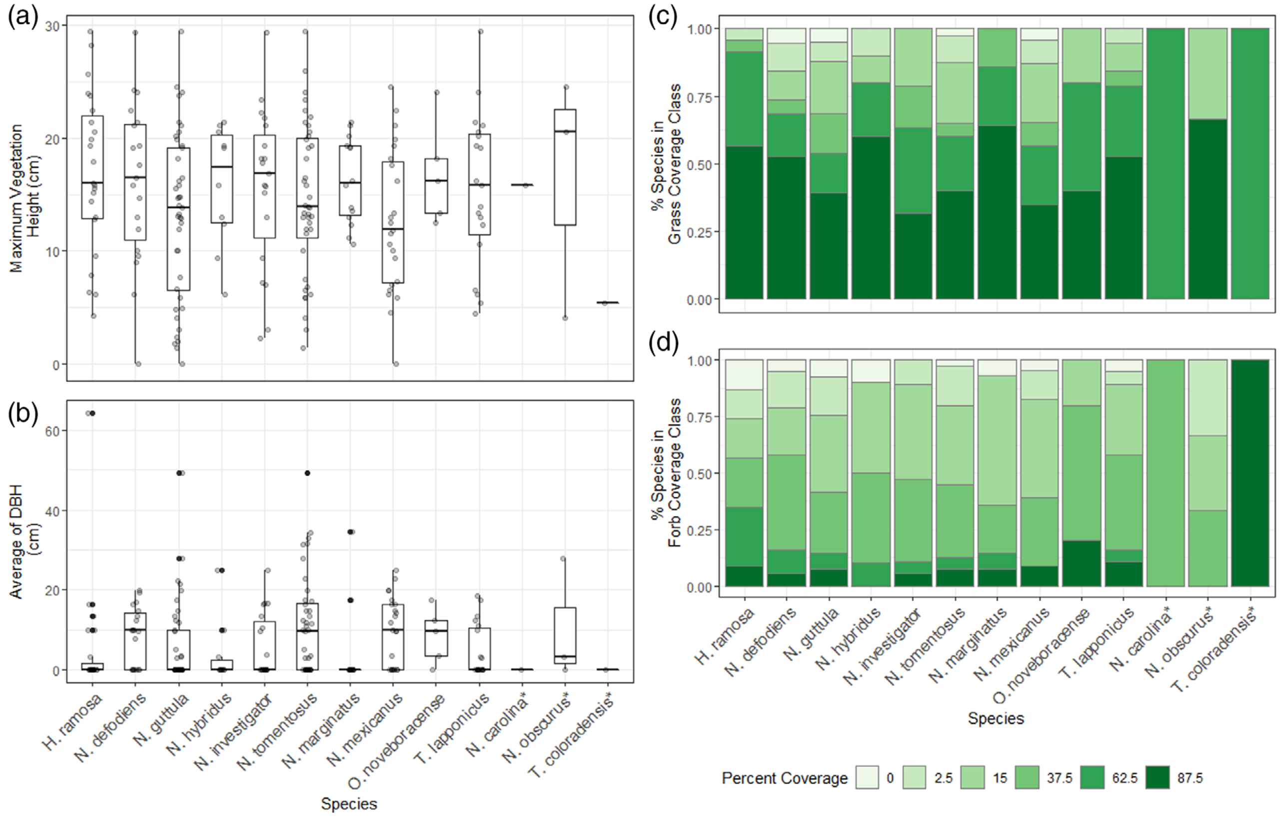

FIGURE 5 Distribution of selected vegetation variables at carrion beetle collection locations shown by species. All species and collections across all ranges, transects and sites are included. Shown are (a) maximum vegetation height in cm, (b) average of DBH in cm, (c) maximum percent coverage of grass and (d) maximum percent coverage of forbs across elevation. Rare species not included in the best model are denoted with a star and have been arranged on the right side of the figure. The three rare species are *N. carolina* ($n = 1$, 1 plot at 1 site), *N. obscurus* ($n = 3$, 3 plots at 1 site) and *T. coloradensis* ($n = 17$, 1 plot at 1 site).

collected from four large elevational gradients, we looked for fidelity in vegetation associations across habitats, sites and mountain ranges. As Colorado carrion beetle diversity and abundance is strongly associated with the density of understory vegetation, we expected that differences in specific vegetation associations would explain much of the spatial pattern in carrion beetle abundance (McCain, 2021). However, we found little evidence of habitat-vegetation affinities among the 14 species of carrion beetle in Colorado assessed here. Instead, we found evidence of substantial niche overlap in habitat and vegetation use. Overall, the vegetation and habitat models explained a much smaller portion of variation in the data than expected. Species' associations with fine-scale vegetation and habitat types explained a maximum of 18.93% of the variation in the data. For all species, models explained 12.83% and 1.6% of the variation in abundance and presence–absences, respectively. For only the non-rare species, models explained 18.93% and 2.48% of the variation in abundance and presence-absences respectively. The large amount of residual variation indicates that vegetation use is likely one of many factors that limit species' similarity and contribute to coexistence in this community (Macarthur & Levins, 1967). Given that most carrion beetle abundance and diversity is found in the wetter, denser vegetation within habitats and across sites, which is generally rare in this arid-dominated region, the co-occupation of those denser vegetation types within habitats create a strong vegetation niche overlap among all species and species within each subfamily (McCain, 2021).

There were few differences in which vegetation attributes were associated with the greatest abundance or presence of each species. Only one species, *Heterosilpha ramosa*, was strongly differentiated from other species as being associated with areas of smaller trees, taller understory vegetation, greater ground cover of grasses and forbs, and riparian habitat. In additional Colorado surveys during 2019–2022, *H. ramosa* was noted as an early season species with high interannual variability in abundance, which may complicate these patterns (Garfinkel & McCain unpublished). The species *Thanatophilus coloradensis*, a rare species that was eliminated from some models, is known to be a high-elevation specialist occurring only above treeline (Peck & Anderson, 1982). The data did show these unique associations with habitat and vegetation characteristics, as *T. coloradensis* was found only in the tundra with high forb coverage and no trees. But given its rarity in this dataset (18 individuals at one plot within 1 site), we were unable to identify this statistically in comparison with other species. In the CCA models, a majority of the species clustered closely together, translating to minor differences in associations with the significant variables. For example, species-averages for DBH spanned 7.16 cm, but the differences among most species was within only 3.68 cm. Most species were collected over the entire range of values for each measured vegetation characteristic, indicating high overlap in vegetation use. Additionally, the ratios of carrion beetle collections among habitat types were fairly similar across all non-rare species, indicating high overlap in habitat use. These differences appear too small to alleviate pressure from intense resource competition and indicate that in Colorado, most species, except possibly *H. ramosa* and *T. coloradensis*, could be classified as habitat generalists. Interestingly, the presence of riparian habitat was the only variable included in all four candidate models, making it likely that associations with riparian habitat and the wetter, denser vegetation are robust to differences in collection methods and the presence of rare species in the dataset.

Previous research has indicated that some North American species have preferences for particular habitat types (Anderson & Peck, 1985; Scott, 1998), including that *Nicrophorus defodiens* (Mannerheim) is a forest species and that *Nicrophorus tomentosus* (Weber) is a forest and grassland species. We found no evidence to support these specific habitat associations or any specialised habitat associations for these species across our more arid dominated transects. The species *N. investigator* has been found to prefer sunny areas to shaded areas for burying carcasses in Colorado (Smith & Heese, 1995), but we found no relationship for general capture occurrences of this species and related vegetation attributes like canopy cover and the number of trees in the plots. A recent study conducted in Ontario, Canada also used fine-scale vegetation characteristics to look for niche partitioning in a carrion beetle community (Burke et al., 2020). Authors also found little evidence of partitioning in fine-scale vegetation characteristics, and species were instead assigned to broad habitat categories and identified as either generalists or specialists. *N. tomentosus* was identified as a habitat generalist, and we also found no specific or consistent habitat or vegetation associations for *N. tomentosus* in Colorado. Burke's analysis of three *Nicrophorus marginatus* (Motschulsky) individuals indicated that it was predominantly a meadow and field species as has been found in previous research (Burke et al., 2020; Dyer & Price, 2013; Keller et al., 2019; Lingafelter, 1995; Lomolino et al., 1995; Smith et al., 2000), but we found no evidence to support a habitat preference of *N. marginatus* in Colorado using 105 individuals collected across these large elevational gradients. At the scale considered here, we found little evidence of fidelity to habitat types or vegetation types across many sites at many elevations. Other studies typically use one site and a few habitat types and are in more productive climates and regions, and this may explain differences between our results and previous work. Additionally, some species may only have habitat preferences during breeding and not during feeding, highlighting issues with traditional sampling methods using baited pitfall traps for habitat studies (Scott, 1998). Baited traps with small amounts of natural or non-natural animal meat to attract carrion beetles may be biased towards feeding behaviour and not reflect size-based preferences for breeding (Scott, 1998; Smith & Heese, 1995). As carrion beetles encounter and use vegetation during times of inactivity, behavioural thermoregulation, predator avoidance and even resource movement and burial, a less biased approach is needed to assess overall movement and behaviour. The traps used in this study were unbaited, potentially reducing bias towards feeding and capturing habitat use during feeding, breeding and species interactions.

It is possible that habitat and vegetation characteristics measured here are at too fine a scale to be important for carrion beetle habitat partitioning based on their movement distances to find vertebrate carcasses. Typical movement distances are unknown for most species of carrion beetle. A species not found in Colorado, *Nicrophorus americanus*, which is the largest Silphid and likely the strongest flier, can move more than 1 km per night but typically moves closer to 1/3 kilometre per night (Bedick et al., 1999; Jurzenski et al., 2011; Peyton, 2003). Despite this, characteristics measured here are undoubtedly at a scale important to carrion beetle use of microclimate and predator refuges. It is also likely that habitat and vegetation characteristics not measured here are important. These data were originally collected to test the more-individuals hypothesis by looking for links between habitat productivity and complexity, food biomass (both vegetation and arthropods) and small mammal abundance and species richness (McCain, 2021; McCain et al., 2018). Since vegetation attributes can affect arthropods serving as a food source for mammals, many characteristics relevant to arthropods were chosen and the set of vegetation characteristics measured was both comprehensive and comparable to similar arthropod studies (Burke et al., 2020; McCain et al., 2018). Additionally, sampling covered four elevational transects in two mountain ranges, with more sites and trap days than any other study of its kind, making it unlikely that we would have failed to capture a trend if one was present. Rather than using baited pitfall trips, this study used unbaited pitfalls, which have been shown to be as successful as baited traps in collecting carrion beetles and are the most commonly used method of arthropod collection (Cheli & Corley, 2010; McCain, 2021). While some studies involve the use of both ground and canopy-level traps, no canopy traps were used in this study design, leaving us unable to determine if these preferences exist in Colorado carrion beetles. However, species previously found to prefer either the canopy or the ground are not present in Colorado (Burke et al., 2020; Wettlaufer et al., 2018). Other habitat and vegetation characteristics that were unmeasured and could be important include surface hardness, soil moisture, light intensity and canopy height (Hoback, 2016; Jakubec & Růžička, 2015; Smith & Heese, 1995; Wettlaufer et al., 2018).

While other studies detected strongly differentiating species–habitat associations, our work detected only weak associations, lending caution to generalising habitat associations across regions and species assemblages. Habitat and species assemblages vary widely across time and space, meaning that specialisation and competitive interactions are different in each community and during each season. In these arid, western mountains, likely the limiting existence of wetter, denser vegetation that is important to all carrion beetle species constrains their ability to finely partition habitat among species. Carrion beetles may specialise in other ways including vertebrate species or size preferences seasonality, daily activity times, body size as it affects competitive interactions, physiological traits and other components of life-history strategy (Futuyma & Moreno, 1988, Feer & Pincebourde, 2005, Kocárek 2001, Collard et al., 2021). Many of these factors are theorised but not consistently shown to prevent or minimise contact between species and therefore reduce competition between them (Anderson & Peck, 1985; Scott, 1998). Unfortunately, these factors are also largely undocumented, thus, were not available for use in this analysis. While mechanisms of coexistence are not yet known in Colorado carrion beetles, we found only slight habitat and vegetation partitioning. Thus, other mechanisms reducing niche overlap must be present in this system to enable the coexistence of these 15 competing species. By understanding how habitat specialisation differs both within and across species assemblages, we will better understand mechanisms underlying species coexistence in beetles and be better equipped to protect their biodiversity as a result.

AUTHOR CONTRIBUTIONS

Project conceptualization: CFG and CMM. Project management and data collection: CMM. Analysis: CFG. Visualisation: CFG and CMM. Writing, review, and editing: CFG and CMM.

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CONFLICT OF INTEREST STATEMENT

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Distribution of habitat types of carrion beetles collected only from unbaited pitfall traps with vertebrate bycatch present.

Figure S2. Distribution of habitat types of carrion beetles collected only from baited pitfall traps.

Figure S3. Distribution of habitat types across all unbaited pitfall traps.

Figure S4. Distribution of selected vegetation variables across elevation.

Datasets S1. Matrix of all species' abundances by sampling plots.

Datasets S2. Matrix of all species' presences (1) and absences (0) by sampling plots.

Datasets S3. Vegetation data by sampling plots.

Datasets S4. Scaled vegetation data by sampling plots.

Appendix S1. Description of methods used to create Figure 3b visualising species' positions along the environmental axes.

Appendix S2. Description of data collection methods for Figures S1 and S2.

Appendix S3. R code for CCA models.

Table S1. Additional canonical correspondence analysis (CCA) results for the abundance model including all species.

Table S2. Additional CCA results for the presence–absence models.

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