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Journal

Frontiers of Biogeography, 0(0)

Author

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Publication Date

2021

DOI

10.21425/F5FBG47013

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Another rejection of the more-individuals-hypothesis: Carrion beetles (Silphidae, Coleoptera) in the Southern Rocky Mountains

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Abstract

Beetles are the most diverse animal clade on the planet, and understanding the mechanisms underlying their diversity patterns is critical to understanding animal biodiversity in general. Using carrion beetles (Silphidae; Coleoptera), I test the more-individuals hypothesis (MIH), consisting of positive climatic impacts on food resources leading to increased abundance and then diversity. I also test competing mechanistic hypotheses, including interacting effects of climate, local vegetation, habitat diversity, habitat heterogeneity, soil diversity, and elevational area. Carrion beetle species richness and abundances were estimated using 40 standardized pitfall traps set for 90 days at 30 survey sites on two elevational gradients in the Front Range and San Juan Mountains, Colorado, USA. Standardized measurements assessed 13 vegetative characteristics, food resources (mammal abundances), soil diversity, habitat diversity, elevational area, temperature, precipitation and net primary productivity at each site. Structural equation models were used to test competing diversity hypotheses and mechanisms. Species richness peaked at intermediate elevations on both gradients, whereas abundance was unimodal on one gradient and decreasing on the other. The MIH mechanism was rejected; all four potential SEM model constructions were unsupported and the majority of all SEM models did not support relationships between abundance and diversity or climate and food resources. The best SEM model included direct influences of temperature, vegetation biomass, and food resources but with separate effects on diversity and abundance. Carrion beetles were more diverse and abundant in sites with dense understory vegetation and warm temperatures, while higher abundances were also linked to more food resources. This climate–biotic relationship is likely due to a need for microclimates and microhabitats to mediate physiological tradeoffs of desiccation and thermoregulation with predation. This suggests a general hypothesis for beetle diversity and abundance, particularly on arid-based mountains globally.

Highlights

- Carrion beetles are a fascinating group of beetles that feed on dead vertebrates, exhibit elaborate parental care, and feature prominently in forensic sciences.
- Carrion beetles are most diverse in the temperate zone and herein found to be most diverse at intermediate elevations in the Southern Rocky Mountains, USA.
- Models unequivocally rejected the more-individuals hypothesis.
- The best model supported a mechanistic relationship of separate, direct influences of temperature and understory vegetation density on diversity, and separate and direct influences of temperature, understory vegetation density, and food resources on abundance.

Keywords: arthropods, carrion beetles, climate-diversity relationship, elevational gradients, food resources, habitat heterogeneity, more-individuals hypothesis, species richness, structural equation modeling, USA

Introduction

Improving our understanding of the patterns and drivers of diversity on the planet is necessary for knowledgeable conservation in times of anthropogenic destruction. Globally and regionally, we have amassed considerable knowledge about the distribution of vertebrate diversity and its strong correlations with climatic energy and productivity (e.g., Currie 1991, Hawkins et al. 2003, Currie et al. 2004, Evans et al. 2005, McCain and Grytnes 2010). However, we are at a standstill in the mechanistic understanding of those relationships (e.g., Storch et al. 2018). Vertebrates are a very narrow slice of animal diversity, only 5%, whereas insects are 80% of described species (e.g., Erwin 1982, May 1988). Beetles (Coleoptera) are the most successful animal clade on the planet with more than 400,000 beetle species described so far (e.g., Stork et al. 2015). Our global and regional understanding of beetle diversity patterns lags enormously behind vertebrates. Beetles, like most clades of insects, are most diverse in the tropics (Erwin 1982), but beyond that our knowledge of patterns and underlying mechanisms for beetle diversity are scant (e.g., Wrenkraud and Ruggiero 2011, Beck et al. 2012; Fattorini 2014, Gebert et al. 2020). Thus, more mechanistic studies on beetles could lead to fresh perspectives and directions.

On mountains, beetle studies focus on identification of new species, changes in morphology, and preliminary elevational analyses (e.g., Darlington 1943, Janzen 1973, Wolda et al. 1998, Herzog et al. 2013, Staunton et al. 2016). Among the beetle elevational richness studies, nearly 100 that I could find in the literature (1953–2019), 75% did not sample sufficiently within and across elevations of undisturbed habitats to detect definitive beetle elevational trends following established review criteria (Wrenkraud and Ruggiero 2011, Szewczyk and McCain, 2016). Nonetheless, the high-quality elevational richness studies for individual beetle clades (e.g., Chrysomelidae; Carabidae; Tenebrionidae) and for those including all beetles (Coleoptera) display the variation in elevational richness patterns shown for vertebrates. Mid-elevation peaks with the highest richness at intermediate elevations and declining at both higher and lower elevations were common (e.g., Lumpkin 1971, McCoy 1990, Nilsson and Persson 1993, García-López et al. 2012, Wrenkraud and Ruggiero 2014, García-Robledo et al. 2016). Declining richness with increasing elevation (e.g., Greenslade 1968, Lobo and Halffter 2000, Fattorini 2014, Wrenkraud and Ruggiero 2014) and lack of a discernable pattern (e.g., Monteith 1985, de Los Santos et al. 2002, Sanders et al. 2010) were also relatively common. The least common patterns were low plateau patterns with high richness across the lower elevations then decreasing at some intermediate elevation with or without a shallow mid-peak (e.g., Botes et al. 2007, Wrenkraud and Ruggiero 2014) and increasing richness with elevation (e.g., Monteith 1985, Olson 1994).

For a sound and deep understanding of biodiversity, both our data and our tests of theory need more focus on beetle diversity. Factors proposed to underlie trends in species richness fall into four broad categories, not

necessarily independently, for all organisms—climate (e.g., temperature, precipitation, productivity), space (e.g., area, bounded spatial extent), evolutionary history (e.g., extinction, speciation, dispersal), and biotic interactions (e.g., food resources, habitat, mutualisms, competition; McCain 2009, McCain and Grytnes 2010, and references therein). For beetle elevational richness, like most organisms, climate factors were the most tested. Due to their ectothermic metabolism, most studies assessed the prediction that beetle richness decreases with elevation as temperature declines (Botes et al. 2007, Fattorini 2014, Wrenkraud and Ruggiero 2014, Gebert et al. 2020). Humidity, precipitation, and/or productivity were also tested in several papers (Greenslade 1968, Sanders et al. 2010, García-López et al. 2012, Gebert et al. 2020). Whereas, spatial trends in area and the mid-domain effect were less tested (Sanders et al. 2010, Fattorini 2014, Gebert et al. 2020). Similarly, models of evolutionary history were rarely proposed and tested with the exception of dung beetles (e.g., Halffter et al. 1995, Lobo and Halffter 2000 and references therein) and climatic stability in flightless carabid beetles (Staunton et al. 2016). As for biotic interactions, essentially single assessments tested influences of vegetation type, diversity or density of vegetation or trees, food resources, or soil variables (Botes et al. 2007, Sanders et al. 2010, Wrenkraud and Ruggiero 2014). The support for all of these hypothesized richness drivers was mixed and conflicting among beetle elevational studies, but the sample sizes were small.

Elevational beetle patterns displaying decreasing richness with increasing elevation correlate with decreasing temperature; whereas mid-elevation peaks in richness often correlate with some form of productivity measurement (Greenslade 1968, Olson 1994, Donlan et al. 2006, Sanders et al. 2010). Thus, for beetles, as for vertebrates, the energy-related climatic factors are most associated with higher richness, and therefore researchers implicitly or explicitly assume some form of the climate–diversity hypothesis (Wright 1983, Currie 1991, Wright et al. 1993, McCain et al. 2018, Storch et al. 2018). The most commonly proposed mechanism for the climate–diversity relationship is the more-individuals hypothesis (MIH). MIH posits that regions with high temperatures or high productivity provide more usable energy, thus leading to greater food resources and larger sustainable population sizes. This results in lower local contemporary extinction rates and therefore the maintenance of greater diversity (Wright 1983, Currie 1991, Wright et al. 1993, Evans et al. 2005, Storch et al. 2018). Most tests of the MIH in the literature only examine the correlation between abundance and diversity (Storch et al. 2018), but recently a few more nuanced studies of all or most links in the mechanism were published on elevational gradients (Ferger et al. 2014, Classen et al. 2015, McCain et al. 2018, Gebert et al. 2020). One of these, on dung beetles (Aphodiinae, Scarabaeinae, Geotrupinae), assessed the competing direct and indirect mechanisms of multiple hypotheses simultaneously, specifically all components of MIH, the species-area effect, and land use (Gebert et al. 2020). In this case, temperature was strongly linked to richness, with a

minor influence of precipitation, but not mediated by food resources, area, or land use. Thus, the MIH mechanism was not well-supported, particularly when food resources were included. Gebert et al. (2020) is the first test of MIH in beetles, but sampling was low within each elevational site (3 pitfalls for 72 hours). Thus, more studies and more deeply sampled datasets are required.

Herein I simultaneously test all four mechanistic links to MIH with three regional climatic variables (temperature, precipitation, and productivity), food resources (mammal abundances), and beetle abundance and diversity. I also test multiple complementing diversity hypotheses by including factors found in other studies to have influenced beetle richness, including various vegetation characteristics, habitat diversity, habitat heterogeneity, soil diversity, and the species-area effect (Fig. 1). I use carrion beetles (Silphidae) as a test clade, because the Southern Rocky Mountains are a hotspot of their diversity and because of their specialist feeding and reproduction on the ephemeral carrion of vertebrates (mostly mammals) that is robustly quantifiable. The sampling regime was deep and broad, using 40 pitfalls for 90 days at each of the 30 sites spread across the elevations of two montane gradients in the Colorado Rocky Mountains, thus representing a valid, robust test of beetle elevational diversity and its drivers.

Materials & Methods

Two elevational transects each with two replicates were established in the Colorado Rocky Mountains in the Front Range (Northeastern Colorado Rockies: NE) and the San Juan Mountains (Southwestern Colorado Rockies: SW; Fig. 2). The Southern Rocky Mountains in the western United States are characterized by arid grassland and desert lowlands, foothill mid-elevations of shrub and Pinon-Pine in the southwest and Ponderosa Pine in the northeast, then mixed conifer and finally alpine and tundra habitats. The San Juan transects are warmer and more arid, particularly at the lower 1/3 of the mountain, than the Front Range, although the middle and high elevations in the San Juans receive more summer precipitation than do the Front Range transects. In the context of carrion beetle (Silphidae) distributions, which are not well documented in the southwestern US, 18 species occur or are purported to occur in Colorado. However, current knowledge anticipates only 15 silphids in the Front Range Mountains and 10–11 in the San Juan Mountains (Appendix S1 in Supporting Information).

To characterize climate, habitat, and organismal changes with elevation, I chose sites every 200–300m of elevation between the base of the range (1400–1700m) and the upper limit of vegetation on the mountaintop (3600–3800m) for each transect (Fig. 2). In total 32 sites were sampled between

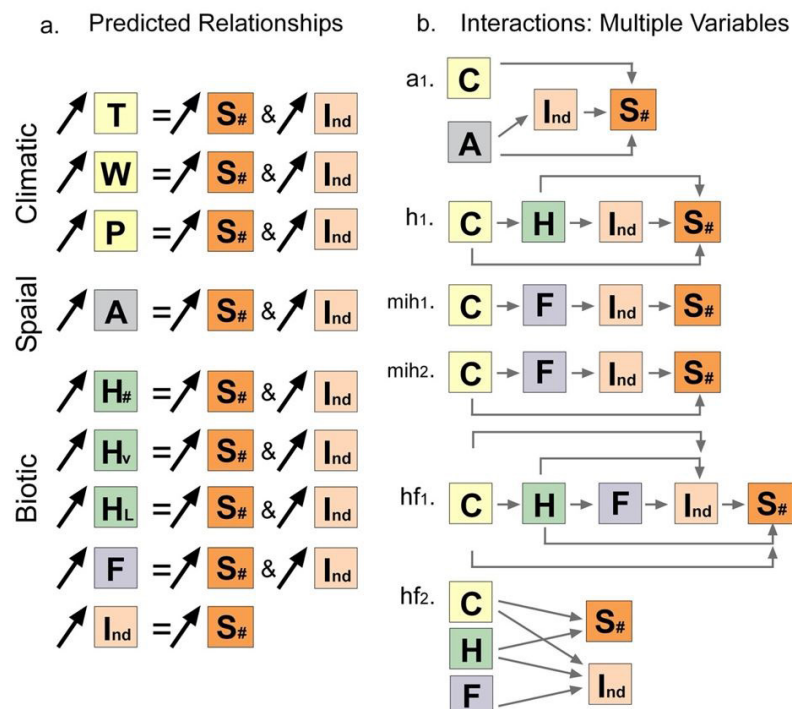


Figure 1. The predicted relationships of various abiotic and biotic drivers of species richness (S#) and abundance (Ind). a. The single, dependent variable associations predicted to increase diversity and abundance with the increase in the variable: climatic (C) = temperature (T); precipitation (W); and productivity (P); spatial = species-area hypothesis (A); biotic-habitat = habitat diversity (H#); habitat heterogeneity (H_v); local habitat measurements (H_L; e.g., vegetation biomass, canopy cover); biotic-food resources = F; biotic-taxon abundance = Ind. b. the hypothesized, multivariate relationships of how climate may interact with area (a1), habitat (h1, hf1, hf2), food (mih1, mih2, hf1, hf2), and abundance (all) to determine diversity.

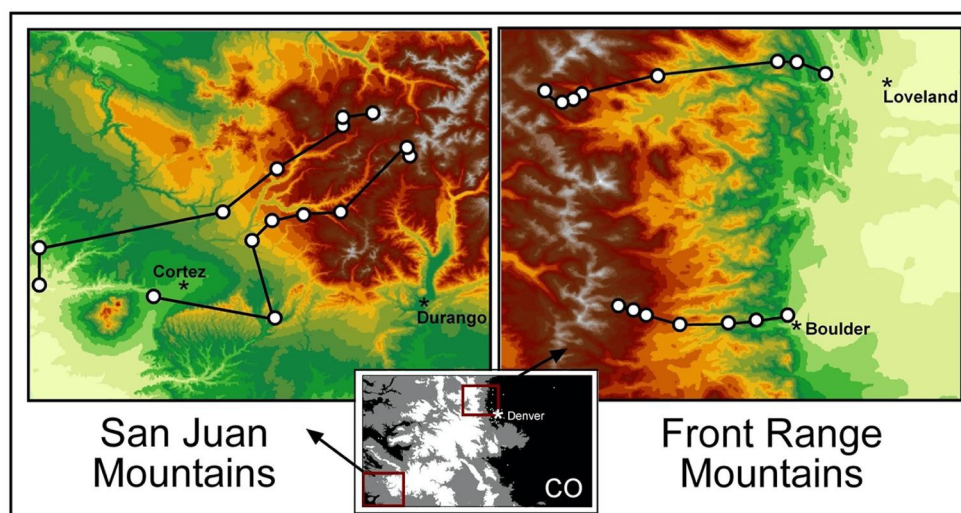


Figure 2. The four elevational transects in the Colorado Rocky Mountains, USA: two in the northeast (Front Range Mountains) and two in the southwest (San Juan Mountains). Each transect included eight sites spread between the base and top of the mountains, although the upper site on two transects were unsuccessful for pitfall traps due to vertebrate disturbance and are not shown. Elevational variation ranges from light green at low elevation to red and grey at higher elevations. The black and white inset is the entire state of Colorado (CO). For scale, the distance between the cities of Boulder and Loveland is about 28.5 miles or 46 kilometers; and between Cortez and Durango is about 39 miles or 63 kilometers.

2010–2012, although only 30 sites were successful for pitfall sampling due to repeated vertebrate disturbance (mostly marmots and bears). I chose sites that included most if not all of the main habitats at that elevation and were relatively undisturbed anthropogenically. At each site, I established sampling lines in proportion to the availability of the main habitat types based on aerial imagery, which across all sites included forest, riparian, meadow, desert, tundra, and rocky outcrops. Pitfall trap pairs were located in a sampling plot every 70 meters along each sampling line consisting of 20 pitfall pairs (40 total) across all habitats per site. I established pitfalls and sampling plots in early summer (mid-May to late June), constrained by the timing of the snowmelt at higher elevations, and sampled for 90 days (~3600 pitfall trap-nights per site). The initial goal of the multiyear project was mammalian diversity and climate change responses, thus ground-dwelling arthropod biomass was measured for mammal food resources. Consequently, pitfall traps were unbaited. Carrion beetles were conspicuous and abundant in the pitfalls (~30% of all sampled Coleopteran individuals) and became a secondary focus of the research during the initial year. The first summer, samples from the pitfalls were collected sporadically as logistics were perfected and thereafter were collected bi-monthly or monthly.

The pitfall traps followed standard entomological design of two nested 470 ml (16 ounce) cups, buried such that the lips were flush with the ground, covered with a small plate leaving a ~3–5cm opening, and filled to ~1/3 to ~1/2 with propylene glycol as a preservative (e.g., Brown and Matthews 2016 and references therein). To increase the surface-area of interception, I radiated three 30 cm wood shims out from the cups. All arthropod samples were cleaned from debris and propylene

glycol, weighed, sorted, counted, and preserved in 70% ethanol. Carrion beetles were identified using a combination of keys available for the species occurring in Colorado and surrounding states (Anderson and Peck 1985, Peck and Kaulbars 1987, Peck and Miller 1993, Ratcliffe 1996, Hanley and Cuthrell 2008, De Jong 2011). Carrion beetle abundance was simply the sum of carrion beetles captured at each site across the three months of sampling. Insect capture abundances are often characterized as a reflection of activity-density, especially for studies with a short sampling window that can be highly influenced by weather conditions (e.g., Greenslade 1964, de los Santos Gómez et al. 2014). Given that pitfalls are the only standardized way to estimate the abundance of carrion beetles, a collecting duration across the entire growing season hopefully minimized the influence of weather and other activity impediments to population estimations.

Since pitfall traps are also used to survey shrews and voles as well as other small vertebrates like frogs, salamanders and lizards, some pitfalls also contained vertebrate bycatch (Fig. S1.2). To compare the influence or potential sampling bias for carrion beetle abundances and diversity with pitfall bycatch, I assessed various site, pitfall, and carrion beetle catch numbers with vertebrate bycatch numbers.

Carrion food biomass

Carrion beetles of both subfamilies predominantly feed upon mammals but also other vertebrates, sometimes dung, fungi, and vegetation (Anderson and Peck 1985, Peck and Kaulbars 1987, De Jong 2011). The Nicrophorine specialize in reproducing on small vertebrate carcasses that they bury, thus they have evolved elaborate social behaviors (Anderson 1982, Scott 1994, Trumbo 1994, Scott 1996). Whereas the Silphinae reproduce and lay their eggs in the soil near

larger mammal carcasses (Anderson 1982, Anderson and Peck 1985, De Jong and Chadwick 1999). I assessed small- to medium-sized mammals (rodents, shrews, pika) abundance and biomass through standardized live-trapping, the pitfalls, and visual surveys at each site. I employed 300 Sherman live-traps along the same sampling lines as the pitfalls. Each site was live-trapped for five nights (1,500 trap-nights) during the reproductive season. For diurnal rodents and pika that do not readily enter live-traps, five visual transect surveys were stratified across time and habitats.

Mammal abundance was a sum of all individuals detected per site, the most common and unbiased assessment of populations for small mammals (Minimum Number Known Alive (MNKA); Wilson et al. 1996, Slade and Blair 2000, Prevedello et al. 2013, McCain et al. 2018). For some species, I detected sufficient recaptures to estimate a species' population size from mark-recapture methods (Nichols and Conroy 1996, Slade and Blair 2000). Since both metrics were highly correlated ($r = 0.975$, $P < 0.001$), I used MNKA. I assume that abundance and biomass of large-sized mammals are relatively equally distributed across the gradients, because all of the larger carnivores (e.g., mountain lions, bear) and ungulates (e.g., deer, elk, bighorn sheep) occur across all elevations and in most cases move widely among elevations (e.g., Armstrong et al. 2011).

Vegetation & habitat

I measured site vegetation characteristics at each of the 20 pitfall sampling plots. Within concentric circles of 1 m, 3 m, and 5 m, vegetation was measured early summer, mid-summer, and late summer. Within the 1 m radius, I estimated ground coverage classes for grasses, forbs, shrubs, cacti, and bare ground within ≤ 1 m height from the soil surface (Braun-Blanquet classes: Cain and De Oliveira Castro 1959, Barbour et al.

1999). Understory vegetation height (≤ 1 m height) was measured at the center point and at the 3 m radius in the four cardinal directions. Additionally, at these same 3 m cardinal directions, I measured canopy coverage using a densiometer. The pitfall traps were placed at the 3 m east and west locations. Species identities, counts, and diameter at breast height (dbh) for trees > 3 cm dbh were recorded within the 5 m radius circle. For an understory vegetation biomass volume, I used the sum of the average (among three visits) understory coverage percentages for forbs, grass, and shrubs multiplied by the average height (among five measurements and three visits). The sum was used to include the influence of divergent times of vegetation maturity among the sites due to elevational variation in the timing and length of the growing season. The habitat heterogeneity metric was calculated as a sum of coefficients of variation for (a) each ground cover type (grass, forb, shrub, cacti, and bare ground), (b) understory vegetation height, (c) canopy cover, and (d) tree diameter at breast height.

Climate, productivity, GIS data

At each site I established a climate station (air and soil temperature, rainfall gauge) that was in place for 12 months. For the watershed surrounding each transect, I calculated mean annual precipitation and temperature from PRISM data (30-year averages; 800 m resolution), and mean annual net primary productivity (NPP ($\text{gC}/\text{m}^2/\text{yr}$); stomatal closure- modified MODIS (Moderate Resolution Imaging Spectroradiometer; NASA Satellite) data (Running et al. 2004; 1 km resolution), averaged for each 100 m band of elevation. Local temperature values were 94–95 percent correlated (correlation coefficients) with PRISM data across sites, but because a few climate stations did not have continuous 12-month collections for both variables, I used the PRISM data for analyses (Fig. 3).

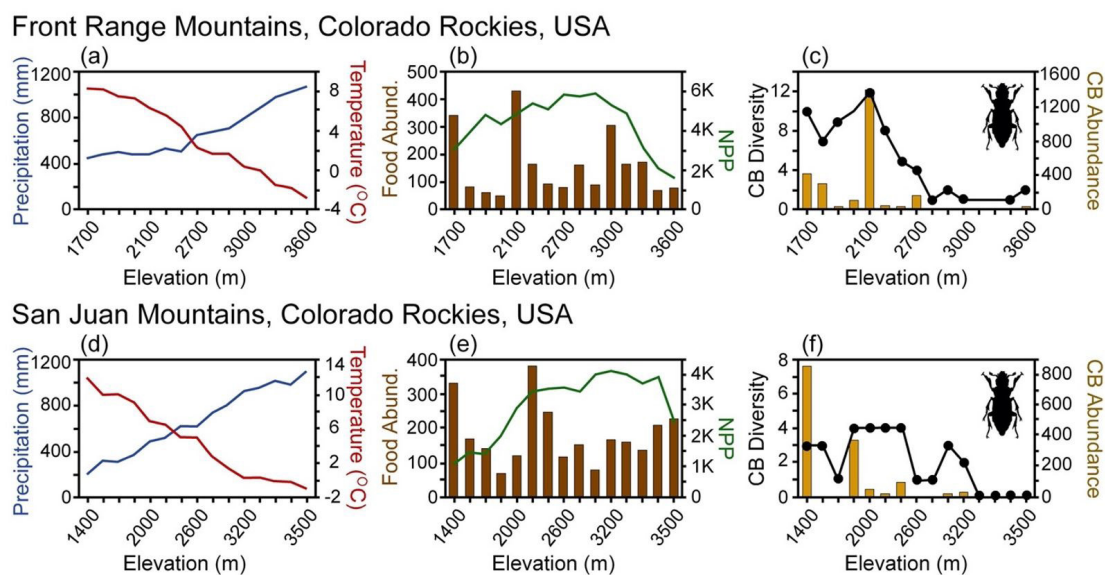


Figure 3. Collected data for testing the more-individuals hypothesis from the two montane regions in the Colorado Rocky Mountains, USA based on 30 sites. (a) & (d): temperature (red lines) and precipitation (blue lines). (b) & (e): primary productivity (NPP = green lines) and mammalian food resources (carion index = brown bars). (c) & (f): Carrion beetle abundance (orange bars) and species richness (black lines).

I measured habitat diversity from the number of land cover types in the elevational band of each site within its watershed using the National Land Cover Database (2011; excluding perennial ice/snow, open water, and human development; 30 m resolution) and a soil type diversity using USDA: STATSGO2 coverage (resolution: rasterized to 30m). For each, I calculated the classical version of Shannon's diversity index within each 100m elevational band (Fig. 4). I tested the species-area relationship using the spatial extent for each 100 m elevational band calculated in an equal area projection of a digital elevational model (90 m resolution) in a GIS following McCain (2007).

Models & Statistical analyses

Based on the proposed theories for diversity (e.g., Wright 1983, Currie 1991, Lomolino 2001, Currie et al. 2004, McCain 2009, and references therein), individual drivers are predicted to be positively related to diversity and abundance (e.g., greater productivity leads to more species and more individuals; Fig. 1a). Based on a mechanistic view of hypothesized drivers of diversity and on the empirical support for multiple variables in most biodiversity studies, I constructed six hypothesized models for how carion beetle diversity and abundance could be driven by a combination of climate, habitat, area, and/or food resources (Fig. 1b). These include the classic representation of the MIH (Fig. 1b: mih1), as well as a modified MIH with an additional direct relationship between climate and diversity (mih2). The area-climate hypothesis (a1) includes direct climate effects on diversity as well as direct and indirect effects of area on abundance and diversity as the species-area effect is often hypothesized to involve decreased extinction rates with higher population sizes in larger areas (e.g., Rosenzweig 1992). Lastly, there are three hypothesized models with climate and habitat, two that are similar to the MIH except the first (h1)

using habitat variables instead of food resources and with added direct effects of climate and habitat on diversity, and the second (hf1) inserting habitat as mediating the relationship between climate and food resources, with additional direct effects of habitat on abundance and diversity. Lastly, the hf2 hypothesis decouples the direct relationship between diversity and abundance, and it only includes direct effects of climate and habitat on diversity and separate direct effects of climate, habitat and food on abundance.

Only variables positively related to diversity (Fig. 1a) and independent variables (correlation coefficient < 0.5) were included in the models. Thus, I calculated a correlation matrix to assess directionality and correlations among all variables: diversity (dependent variable) and the independent variables: abundance (dependent in hf2), temperature, precipitation, productivity, area, habitat diversity, soil diversity, habitat heterogeneity, understory vegetation biomass, canopy cover, and food resources. In the hypothesized relationships (Fig. 1b), the particular climate and habitat variable could be chosen among several possibilities. Thus, the highest fit variable is used initially, then a second model with two variables (fit was assessed from the correlation coefficient with diversity).

To test the causal support of the six hypothesized model mechanisms (Fig. 1b), I constructed structural equation models (SEM; Grace 2006, Grace et al. 2014) using the lavaan package (Rosseel 2012) in R. All variables were z-transformed to a mean of zero and a standard deviation of one, so that variables were of a comparable magnitude. To keep all values positive, I added a constant. I based the initial SEM model fit on the Chi-square test, which compares the empirical data structure to the hypothesized structure. Only models with non-significant tests are viable since non-significant test values indicate an agreement between the observed data and the theoretical model depicted in the path diagram (e.g., Shipley 2000, Schermelleh-

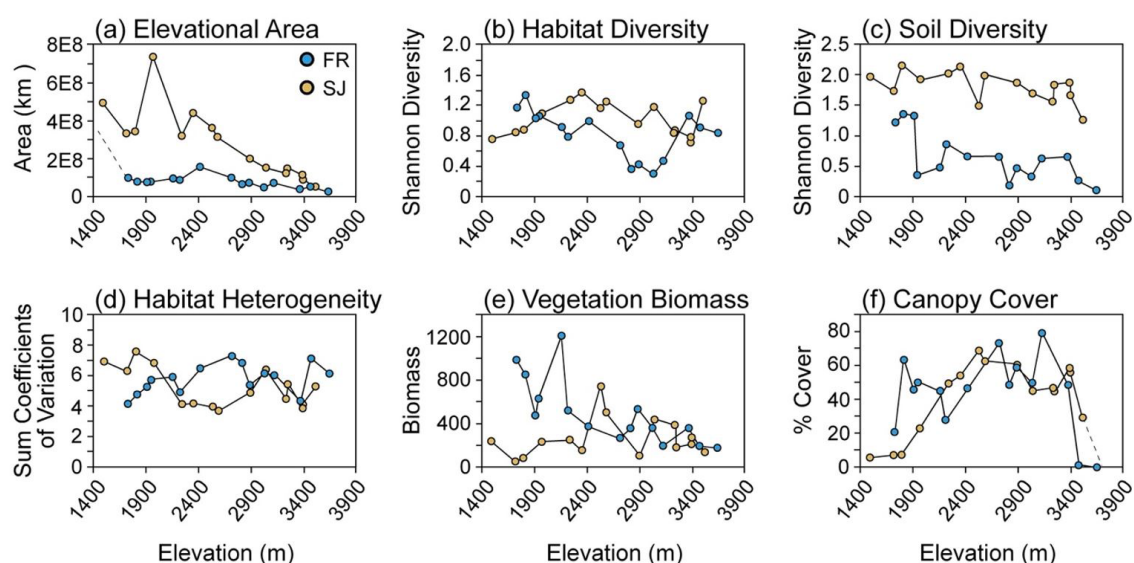


Figure 4. Abiotic (a. area, c. soil diversity) and biotic (habitat diversity, habitat heterogeneity, vegetation biomass, and canopy cover) variables hypothesized to influence carion beetle diversity and abundance from 30 sites along the two regional elevational gradients in the Colorado Rocky Mountains, USA: Front Range Mountains (FR) and San Juan Mountains (SJ).

Engel et al. 2013). To compare model quality, I used a multi-index approach for non-saturated models with model quality determined by cutoff values (in parentheses): Comparative Fit Index (CFI > 0.95; high values indicate good models), Standardized Root Mean Square Residual (SRMR < 0.1; this and all following metrics: low values indicate good models), Root Mean Square Error of Approximation (RMSEA < 0.08), and the AIC value (Browne and Cudeck 1992, Hu and Bentler 1999, Shipley 2000, Grace 2006, Kline 2010, Schermelleh-Engel et al. 2013). The best quality model was assessed according to the combination of the Chi-square test and the four indices (Schermelleh-Engel et al. 2003). The models were replicated separately for each subfamily (Nicrophorinae; Silphinae) to examine consistency of model fits. Model parameters, standard errors, and individual p-values are presented for comparison, interpretation, and repeatability (e.g., Shipley 2009).

Results

I detected 3886 individuals of 15 carrion beetle (Silphidae) species, including nine from the subfamily Nicrophorinae and six from the subfamily Silphinae (Fig. S1.1). Silphid elevational species richness peaked at mid-elevations on both mountains, although lower in the foothills in the Front Range and closer to mid-mountain in the more arid San Juans (Fig. 3). The diversity patterns of each subfamily mirrored the combined elevational diversity pattern per mountain ($r = 0.84\text{--}0.97$, $p < 0.001$). Temperature declined and precipitation increased with elevation on both mountains (Fig. 3a, d), while regional NPP was unimodal with maximum productivity at upper mid-elevations (Fig. 3b, e). Elevational area, habitat diversity and heterogeneity, soil diversity, understory vegetation biomass, and canopy coverage varied among elevations and mountains from declining and increasing trends to bimodal and unimodal trends (Fig. 4). Carrion beetle and mammal abundance were also variable across elevations (Fig. 3). The entirety of the dataset is openly accessible (Appendix S2).

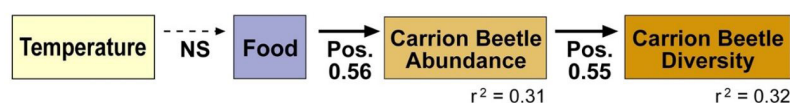
Sampling bias in carrion beetle diversity and abundance could result from differential numbers of pitfalls with vertebrate bycatch by potentially attracting more silphid individuals, but all analyses indicate this is not the case herein (Appendix S1). There is no relationship between sites with greater pitfall bycatch and silphid diversity ($r^2 = 0.0009$, $p = 0.875$) or abundance ($r^2 = 0.020$, $p = 0.463$). Most pitfalls with bycatch (86%) did not catch any carrion beetles. And in the past several years, using baited pitfall trapping for carrion beetles along these gradients and at many of the same sites, elevational diversity patterns remain unchanged (Fig. S1.1; Front Range $r = 0.947$, $p < 0.0001$; San Juans $r = 0.861$, $p < 0.0001$).

Hypotheses testing

The correlation matrix (Table 1) detected multiple variables that were negatively related to carrion beetle diversity, including precipitation, area, soil diversity, habitat heterogeneity, and canopy cover. Additionally, several variables were highly correlated, but these coincided with those that were negatively related to diversity. Thus, the two climate variables included in the models were temperature and productivity; the two habitat variables included were habitat diversity and understory vegetation biomass; and finally food resources. Area and the climate-area hypothesis (a1) were both rejected *a priori* since greater elevational area did not result in more species of carrion beetles.

The Chi-square test detected poor fits between the empirical data structure and the hypothesized model structure in three of the four more-individuals hypothesis (MIH) models as well as in simpler climate-habitat models (Table 2). The final modified MIH model did not meet any of the quality criteria for a strong model fit. Additionally, 60% of the models including a direct effect of abundance on diversity and all four models including a direct effect of climate on food resources failed to detect those relationships. Thus, MIH is unsupported as a mechanism for carrion beetle diversity and abundance across multiple measures (e.g., Fig. 5a; Table 2).

(a) More Individuals Hypothesis:



(b) Climate-Habitat-Food [Best Model]:

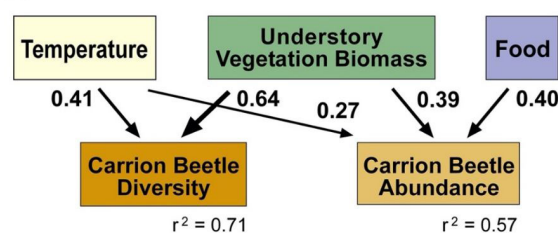


Figure 5. Two competing causal models for drivers and relationships between carrion beetle species richness and abundance based on 30 sampled sites along elevational gradients in the Southern Rocky Mountains of Colorado and their support based on structural equation models (SEM). (a) The mechanistic model for the more-individuals hypothesis (MIH) was rejected based on SEM statistics, and (b) the best-supported SEM model, which included three independent variables with separate richness and abundance relationships. See Tables 1 & 2, Appendix 3 & 4 for all SEM model statistics.

Table 1. Correlations among variables theoretically linked to higher carrion beetle diversity or abundance along four elevational gradients (30 sites) in the Southern Rocky Mountains of Colorado, USA. All relationships with diversity (#Species) and abundance (Inds) are predicted to be positive (e.g., increasing food results in more species and abundance), hence negative variables were not used in models (gray). Additionally, highly correlated variables are not independent, thus only one is used in models (unused = gray). Abbreviations: Temp = temperature; Prec = precipitation; Prod = productivity (NPP); Hab# = habitat diversity; SoilDiv = soil diversity; HabHet = habitat heterogeneity; Veg = understory vegetation biomass; Canopy = canopy coverage; Food = food resources.

Variable	#Species	Inds	Temp	Prec	Prod	Area	Hab#	SoilDiv	HabHet	Veg	Canopy
Inds	0.56										
Temp	0.56	0.44									
Prec	-0.58	-0.44	-0.97								
Prod	0.22	-0.08	-0.15	0.01							
Area	-0.04	0.20	0.65	-0.61	-0.42						
Hab#	0.31	0.07	0.32	-0.18	-0.35	0.31					
SoilDiv	-0.19	-0.04	0.47	-0.32	-0.35	0.66	0.51				
HabHet	-0.05	0.16	0.12	-0.24	-0.09	0.11	-0.44	-0.33			
Veg	0.75	0.59	0.26	-0.28	0.38	-0.21	0.17	-0.26	-0.25		
Canopy	-0.03	-0.16	-0.04	-0.01	0.73	-0.09	-0.05	0.07	-0.33	0.24	
Food	0.18	0.56	0.24	-0.22	0.00	0.16	-0.01	0.14	-0.18	0.31	0.05

The only structural equation models (SEM) with non-significant Chi-square tests and strong fits based on the various SEM indices were the climate-habitat-food models (hf1, hf2) with various constructions of climate, habitat, and food resource influences on diversity and abundance of carrion beetles (Table 2). Only the hf2 models with direct variable effects constructed separately for diversity and abundance met the quality criteria for all four indices. But in two of these cases, negative relationships were detected with one or more variables and carrion beetle abundance. Therefore, the best-fit model was hf2a (Fig. 5b) with direct effects of temperature and vegetation biomass on carrion beetle diversity (Fig. 6) and separate direct effects of temperature, vegetation biomass, and food resources on carrion beetle abundance. For each SEM model, the parameter construction, estimated strength, error and individual significance tests are detailed in Appendix S4. Although not included in the a priori model constructions, adding separate effects of abundance or food to diversity in hf2a did not improve the model or indices: both remained insignificant when included (abundance: $p = 0.910$; food resources: $p = 0.317$) and food resources was negatively related to diversity.

Nearly identical results were supported for each subfamily: Silphinae and Nicrophorine (Appendix S3). Their correlation matrices excluded the same negative and correlated variables as in Silphidae as a whole with the exception of a positive relationship between diversity and habitat heterogeneity in Silphinae (Appendix S1). Thus, the second best local habitat variable in Silphinae models included habitat heterogeneity in place of habitat diversity that was included in Silphidae and Nicrophorinae models. The MIH models as well as the simpler area-habitat and climate-habitat were all rejected for both subfamilies (Appendix S3, S4). The best-fit subfamily

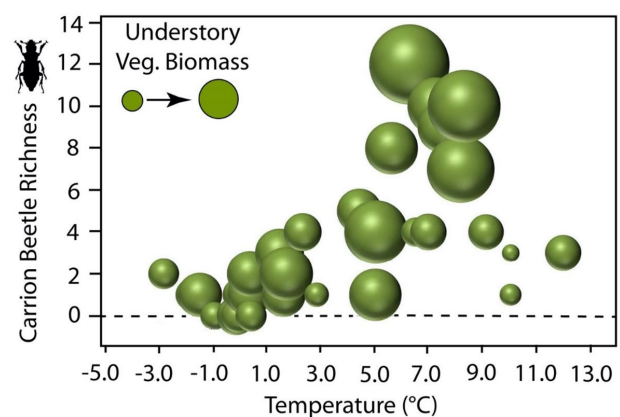


Figure 6. For the 30 sites along the two regional elevational transects in the Colorado Rocky Mountains, the strongest relationships with carrion beetle species richness were an interaction of understory vegetation density (ball diameter) and temperature ($r^2 = 0.71$, $p < 0.0001$) that peaked at lower-middle elevations.

models were also climate-habitat-food models with direct variable effects constructed separately for diversity and abundance. For both subfamilies, like in Silphidae, diversity included direct effects of temperature and vegetation biomass, whereas the two models differed slightly in drivers of abundance (Appendix S3, S4). Specifically, Silphinae included separate direct effects of temperature, vegetation biomass, habitat heterogeneity and food resources on abundance, whereas Nicrophorinae included only direct effects of vegetation biomass and food resources on carrion beetle abundance.

Discussion

Rocky Mountain carrion beetles are most diverse at middle elevations on both mountains (Fig. 3) as well as

Table 2. Comparison of SEM models for carrion beetle diversity and abundance along four elevational gradients ($n = 30$ sites) in the Southern Rocky Mountains of Colorado, USA based on hypothesized models in Figure 1. The climate and habitat variables used in each model are listed and chosen as best-fit variable and second best. A viable model is indicated with a non-significant Chi-square p-value (bold type). Stronger SEM model fits, also bolded, include CFI > 0.95; SRMR < 0.1; RMSEA < 0.08; and the smallest AIC value. Models with negative relationships with diversity or abundance are highlighted with AIC values in gray. The best model based on all comparative statistics is hf2a. Partial MIH predicted relationships, which were unsupported in various models are listed in the last column: A = no relationship between individuals and diversity; B = no relationship between climate and food resources.

Silphidae Model (see figure 1)	Climate	Habitat	Div R^2	Abund R^2	Chi-sqr p-value	CFI	SRMR	RMSEA	AIC	MIH partial rel.
a1 = area & climate	Temp		--	--	--	--	--	--	--	
h1a = habitat & climate	Temp	Veg Biomass	0.713	0.343	0.035	0.932	0.099	0.339	217.831	A
h1b = habitat & climate	Temp, NPP	Veg Biomass	0.724	0.343	0.027	0.913	0.111	0.294	212.481	A
h1c = habitat & climate	Temp, NPP	Veg, Hab#	0.732	0.355	0.001	0.824	0.124	0.379	296.919	A
mih1a = classical mih	Temp		0.319	0.308	0.006	0.685	0.196	0.324	241.545	B
mih1b = classical mih	Temp, NPP		0.319	0.308	0.001	0.541	0.173	0.333	243.538	B
mih2a = modified mih	Temp		0.377	0.308	0.039	0.850	0.131	0.274	237.611	B
mih2b = modified mih	Temp, NPP		0.533	0.308	0.084	0.899	0.109	0.201	232.563	B
hf1a = climate, habitat, food	Temp	Veg Biomass	0.713	0.528	0.153	0.970	0.083	0.171	209.445	A
hf1b = climate, habitat, food	Temp, NPP	Veg Biomass	0.725	0.549	0.099	0.962	0.074	0.209	204.214	A
hf1c = climate, habitat, food	Temp, NPP	Veg, Hab#	0.734	0.632	0.021	0.912	0.089	0.273	202.308	A
hf2a = climate, habitat, food	Temp	Veg Biomass	0.714	0.570	0.321	1.000	0.026	0.000	121.236	
hf2b = climate, habitat, food	Temp, NPP	Veg Biomass	0.725	0.596	0.407	1.000	0.018	0.000	121.684	
hf2c = climate, habitat, food	Temp, NPP	Veg, Hab#	0.738	0.640	0.559	1.000	0.010	0.000	119.524	

on both elevational replicates on each mountain. Over the past decade, in the entirety of carrion beetle trapping (baited and unbaited), these patterns hold true with their maximum diversity at 2100m in the northeastern Front Range Mountains and 2400m in southwestern San Juan Mountains (Fig. S1.1). Are mid-elevational peaks in diversity the norm for silphids? We do not know. Four other elevational studies on the family were conducted (Lumpkin 1971, Martin 1989, Halffter et al. 1995, Lee et al. 2012). Three studies detected highest diversity at middle or high elevations, but were insufficiently sampled to detect a robust pattern (<70% of the elevational gradient sampled, no sampling in the lowest 300 m of

the gradient, and only a few pitfalls per site for a short sampling duration) and most of these were low diversity (4 to 6 species), and included sites with significant human habitat disturbance (Martin 1989, Halffter et al. 1995, Lee et al. 2012). Lumpkin's (1971) unpublished Master's thesis on the silphids of southeastern Tennessee (10 species detected), including the Great Smoky Mountains, also detected a mid-elevational peak in diversity with a relatively robust sampling effort. Unfortunately, the lowest three sites were near population centers (e.g., University of Tennessee campus), and the low diversity may reflect this disturbance.

Silphid natural history is strongly linked to their food resources—mostly mammal carrion—for both feeding and reproduction. Thus, silphids are a robust test system for the more-individuals hypothesis (MIH) or the more encompassing climate-diversity hypothesis, which both posit that greater energy results in greater food resources, thus increasing the abundance of the community that can support more species long term. But the MIH mechanism can be rejected in this case because climate and food resources (mammal abundance) were unrelated (temperature-food: $r^2 = 0.05$, $p = 0.19$; precipitation-food: $r^2 = 0.05$, $p = 0.22$; productivity-food: $r^2 < 0.0001$, $p = 0.99$) and unsupported in any structural equation model (Fig. 5a; Appendix S3, S4). In fact, all SEM models for MIH were rejected based on the model evaluation criteria. The only other beetle elevational study to thoroughly assess MIH also detected a missing relationship between food resources (mammal abundance = dung index) and dung beetle abundance and diversity (Gebert et al. 2020). Additionally, the best supported SEM models included separate and unlinked relationships for carrion beetle diversity and abundance, suggesting a completely different mechanism for diversity than through abundance (Table 2). Similarly, bees, birds, and small mammals showed no or only weak support for MIH (Ferber et al. 2014, Classen et al. 2015, McCain et al. 2018).

The combined lack of support for MIH in mechanistic models across studies suggests a rejection or reevaluation of the theory (e.g., McCain et al. 2018, Storch et al. 2018). Before such a wholesale dismissal, two methodological caveats are necessary. First, although the sampling was deep (40 pitfalls per site for 90 days) and broad (30 sites across four elevational gradient replicates), temporally it was abbreviated—only one growing season sampled per site. As shown in simulations, high interannual variability in abundance can mask the detection of a “true” modelled MIH mechanism (Vagle and McCain 2020). Ideally, 5 to 10 years of data from each of these sites would be necessary to assess if long-term food abundance and beetle abundance averages lead to improved MIH support. However, this is prohibitive financially and logistically as well as for the collecting pressure on the Silphid communities themselves. Contradictory to such a possibility, small mammal abundance (i.e., carrion food) was relatively high above 2800 m, but there are only three beetle species at those elevations and at low numbers across all years of sampling (Fig. S1.2). Because small mammals are most diverse in these mountains between 2400–2600m and consistently abundant at the mid- to high-elevations (McCain et al. 2018), it is doubtful that the food resources trend was a misrepresentative sample in this case. Second, Storch et al. (2018), suggested that MIH might only function at larger (e.g., biome) scales due to the impact of dispersal among populations at small scales obfuscating the relationship between abundance and diversity. This is unlikely to be the case herein, as the current scale is regional or elevational biomes, and the distance among sites is much larger than individual beetle dispersal distances.

The evidence is overwhelming that the diversity and abundance of Rocky Mountain carrion beetles is strongly associated with understory vegetation density (Fig. 5, 6) and this is not part of the MIH mechanism. Nor was a modified MIH through understory vegetation rather than food (h1 a-c) or in addition to food (hf1 a-c) supported by the SEM models (Appendix S3, S4). Interestingly, this vegetation trend would have been difficult to detect along a single gradient because high-density understory vegetation was a relatively rare feature across the Rocky Mountain environment. Vegetation density was also strongly linked to both Tenebrionidae (darkling beetles) and Carabidae (ground beetles) diversity in the Cederberg Mountains of South Africa (Botes et al. 2007). Across other beetle studies at various spatial scales, vegetation density has been important to structuring communities (e.g., Ayal and Merkl 1994, Hosoda 1999, de Los Santos et al. 2002). So why might it be so critical for carrion beetle diversity and abundance? Like for all beetles, it may offer greater cover to escape from predation as well as a variety of microhabitats for activity and resting (e.g., Stapp 1997). For silphids specifically, and all beetles generally, it could reflect the importance of high microclimate humidity. Higher humidity would keep the carrion resource from desiccating too quickly (Bedick et al. 2006, Santos et al. 2011) and may allow the burying beetles (Nicrophorinae) to access consistently moister soils that are easier to dig reproductive chambers and potentially cultivate the antifungal and antibacterial components of the brood carcass preservatives (e.g., Jacques et al. 2009).

The importance of the interplay between understory vegetation and climate was not a simple link to primary productivity (herein measured as NPP; Fig. 3). NPP was also unimodal, but with a much higher maximum toward the upper third of each mountain. Temperature was the second strongest factor for carrion beetle diversity (Fig. 3 & 4), which was negatively collinear with precipitation, thus also likely important (Fig. 3). On both mountains, maximum diversity occurred at elevations with an annual average temperature of 6–9°C and annual precipitation of 450–550 mm. Elevations below that were more arid, particularly so at the lower portions of the San Juans. Silphids clearly do not widely utilize arid environments, evidenced by only three species detected in the desert habitats (Fig. S1.1). Only one of those, *Nicrophorus guttula*, was abundant and is the only species known to be desert associated (Anderson and Peck 1985, Peck and Kaulbars 1987). Carrion beetles, like all beetles, are susceptible to desiccation (Chown 2001, Bedick et al. 2006) and have differential abilities for thermoregulation (Chown 2001, Merrick and Smith 2004), thus the hottest arid habitats may be uninhabitable for most species. This also suggests another important reason for the high diversity and high abundances at middle elevations in thick vegetation. It is warm enough for sustained activity, feeding, and reproduction (e.g., development times: Smith and Heese 1995; and microbial secretions: Jacques et al. 2009), but the thick vegetation provides cooler and more humid microclimates to avoid desiccation of themselves as well as of their food resources.

And, indeed, increased food resources were linked to increased carrion beetle abundances, just not directly to diversity. Such an association might exist for all beetle species across these gradients for similar reasons, thus suggesting that understory vegetation density may play an important role for ground beetle diversity on arid or semi-arid based mountains.

This is the first study to examine definitively the elevational diversity and abundance patterns of the carrion beetles. It is also unusual in that it detected a mechanism that acts separately and independently for diversity and abundance, suggesting that indeed the number of species sustained in a location is not directly related to abundance. Also, it was surprising that a specific habitat characteristic—density of the understory vegetation—as the primary determinant of diversity and abundance since most elevational and latitudinal diversity trends, especially in vertebrates, are primarily linked to climate factors (e.g., Hawkins et al. 2003, Currie et al. 2004, McCain and Grytnes 2010). The interplay of vegetation density, temperature and aridity appear to be driven by a potential combination of differential microclimate and microhabitat effects on the thermoregulatory, desiccation, predator avoidance and reproductive impacts among species. This likely could be similar across all beetles, which could also be examined in the future as all Coleopterans in the samples were also preserved. The intriguing next question is how all of these carrion beetle species can coexist eating and reproducing on the same food resources in the same environment. For example, all 15 species were detected at a single site and most of their ranges are largely overlapping (Fig. S1.1). This is an important question for beetle diversity patterns and biodiversity in general—how can such an extraordinary number of species have evolved and sustained coexistence in single places on the earth? Likely, a better understanding of beetle diversity and coexistence through additional field studies and lab experimentation will illuminate a topic that has come to somewhat of an empirical and theoretical standstill in vertebrates.

Acknowledgements

This work was funded through the National Science Foundation (McCain: DEB 0949601) and would not have been possible without the many extraordinary field and lab assistants, including multiple years of assistance from Holly D'Oench, Hayden Gardner, John Hackemer, Jake Harris, Sarah King, Angela Knerl, Kevin Bracy Knight, Richard Parkhill, Daniella Ramos, Emma Shubin, Emily Braker, Grant Vagle, and Tim Szewczyk. Fieldwork methodology was approved by the CU Boulder IACUC (08-07-McC-02; 1103.02; Protocol 2548) as well as Rocky Mountain National Park, Sylvan Dale Guest Ranch, City of Boulder Open Space and Mountain Parks, Boulder County Open Space, Roosevelt and Arapaho National Forest, The CU Mountain Research Station and Niwot Ridge LTER, San Juans BLM and National Forest Service, Mesa Verde National Park, and Lizardhead Wilderness.

Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>

Appendix S1. Figures S1.1–S1.3. Collected data for testing various competing hypotheses for elevational diversity of carrion beetles at sites; the elevational ranges of carrion beetles based on all baited and unbaited sampling; the relationship between carrion beetle diversity and abundance with vertebrate pitfall.

Appendix S2. Complete dataset for each carrion beetle survey site.

Appendix S3. Carrion beetle SEM model comparisons for Silphidae, Silphinae, and Nicrophorinae, including multiple measures of model fit.

Appendix S4. Carrion beetle SEM model comparisons (Silphidae, Silphinae, Nicrophorinae) displaying the model construction, estimated strength, error, and significance values of each included variable.

References

- Anderson, R.S. (1982) Resource partitioning in the carrion beetle (Coleoptera: Silphidae) fauna of Southern Ontario: ecological and evolutionary considerations. *Canadian Journal of Zoology*, 60, 1314–1325.
- Anderson, R.S. & Peck, S.B. (1985) Part 13: the carrion beetles of Canada and Alaska. The insects and arachnids of Canada. Biosystematics Research Institute, Ottawa, Canada.
- Armstrong, D.M., Fitzgerald, J.P. & Meaney, C.A. (2011) *Mammals of Colorado*, 2nd edn. University Press of Colorado, Denver, USA.
- Ayal, Y. & Merkl, O. (1994) Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel. *Journal of Arid Environments*, 27, 347–361.
- Barbour, M.G., Burk, J.H., Pitts, W.D., Gilliam, F.S. & Schwartz, M.W. (1999) *Terrestrial plant ecology*, 3rd edn. Benjamin/Cummings, Menlo Park, USA.
- Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., et al. (2012) What's on the horizon for macroecology? *Ecography*, 35, 673–683.
- Bedick, J.C., Hoback, W.W. & Albrecht, M.C. (2006) High water-loss rates and rapid dehydration in the burying beetle, *Nicrophorus marginatus*. *Physiological Entomology*, 31, 23–29.
- Botes, A., McGeoch, M.A. & Chown, S.L. (2007) Ground-dwelling beetle assemblages in the northern Cape Floristic Region: patterns, correlates and implications. *Austral Ecology*, 32, 210–224.

- Brown, G.R. & Matthews, I.M. (2016) A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. *Ecology and Evolution*, 6, 3953–3964.
- Browne, M.W. & Cudeck, R. (1992) Alternative ways of assessing model fit. *Sociological Methods & Research*, 21, 230–258.
- Cain, S.A. & De Oliveira Castro, G.M. (1959) *Manual of vegetation analysis*. Harper & Brothers Publishers, New York, USA.
- Chown, S.L. (2001) Physiological variation in insects: hierarchical levels and implications. *Journal of Insect Physiology*, 47, 649–660.
- Classen, A., Peters, M.K., Kindeketa, W.J., Appelhans, T., Eardley, C.D., Gikungu, M.W., Hemp, A., Nauss, T. & Steffan-Dewenter, I. (2015) Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania? *Global Ecology and Biogeography*, 24, 642–652.
- Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, 137, 27–49.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134.
- Darlington, P.J. (1943) Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs*, 13, 37–61.
- De Jong, G.D. (2011) Distribution of the carrion beetle *Oiceoptoma noveboracense* (Förster) (Coleoptera: Silphidae) in Colorado, U.S.A. *The Coleopterists Bulletin*, 65, 438–439.
- De Jong, G.D. & Chadwick, J.W. (1999) Decomposition and arthropod succession on exposed rabbit carrion during summer at high altitudes in Colorado, USA. *Journal of Medical Entomology*, 36, 833–845.
- de Los Santos, A., de Nicolás, J.P. & Ferrer, F. (2002) Habitat selection and assemblage structure of darkling beetles (Col. Tenebrionidae) along environmental gradients on the island of Tenerife (Canary Islands). *Journal of Arid Environments*, 52, 63–85.
- de los Santos Gómez, A., Nicolás, J.P.D. & Dorta-Guerra, R. (2014) Abundance, biomass and diversity of ground-beetles (Col. Carabidae) as indicators of climatic change effects over elevation strata in Tenerife (Canary Islands). *Ecological Indicators*, 46, 504–513.
- Donlan, C.J., Berger, J., Bock, C.E., et al. (2006) Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *The American Naturalist*, 168, 660–681.
- Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin*, 36, 74–75.
- Evans, K.L., Greenwood, J.J.D. & Gaston, K.J. (2005) Dissecting the species–energy relationship. *Proceedings of the Royal Society*, 272, 2155–2163.
- Fattorini, S. (2014) Disentangling the effects of available area, mid-domain constraints, and species environmental tolerance on the altitudinal distribution of tenebrionid beetles in a Mediterranean area. *Biodiversity and Conservation*, 23, 2545–2560.
- Ferger, S.W., Schleuning, M., Hemp, A., Howell, K.M. & Böhning-Gaese, K. (2014) Food resources and vegetation structure mediate climatic effects on species richness of birds. *Global Ecology and Biogeography*, 23, 541–549.
- García-López, A., Micó, E. & Galante, E. (2012) From lowlands to highlands: searching for elevational patterns of species richness and distribution of scarab beetles in Costa Rica. *Diversity and Distributions*, 18, 543–553.
- García-Robledo, C., Kuprewicz, E.K., Staines, C.L., Erwin, T.L. & Kress, W.J. (2016) Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. *Proceedings of the National Academy of Sciences USA*, 113, 680–685.
- Gebert, F., Steffan-Dewenter, I., Moretto, P. & Peters, M.K. (2020) Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. *Journal of Biogeography*, 47, 371–381.
- Grace, J.B. (2006) *Structural equation modeling and natural systems*. Cambridge University Press, Cambridge, UK.
- Grace, J.B., Adler, P.B., Stanley Harpole, W., Borer, E.T. & Seabloom, E.W. (2014) Causal networks clarify productivity–richness interrelations,

- bivariate plots do not. *Functional Ecology*, 28, 787–798.
- Greenslade, P.J.M. (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, 33, 301–310.
- Greenslade, P.J.M. (1968) Habitat and altitude distribution of Carabidae (Coleoptera) in Argyll, Scotland. *Transactions of the Royal Entomological Society of London*, 120, 39–54.
- Halffter, G., Favila, M. & Arellano, L. (1995) Spatial distribution of three groups of Coleoptera along an altitudinal transect in the Mexican Transition Zone and its biogeographical implications. *Elytron*, 9, 151–185.
- Hanley, G.A. & Cuthrell, D.L. (2008) *The Carrion Beetles of North Dakota*. Minot State University, Minot, ND, USA.
- Hawkins, B.A., Field, R., Cornell, H.V., et al. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.
- Herzog, S.K., Hamel-Leigue, A.C., Larsen, T.H., Mann, D.J., Soria-Auza, R.W., Gill, B.D., Edmonds, W.D. & Spector, S. (2013) Elevational distribution and conservation biogeography of Phanaeinae dung beetles (Coleoptera: Scarabaeinae) in Bolivia. *PLoS ONE*, 8, e64963.
- Hosoda, H. (1999) Elevational occurrence of ground beetles (Coleoptera, Carabidae) on Mt. Kurobi, central Japan, with special reference to forest vegetation and soil characteristics. *Pedobiologia*, 43, 364–371.
- Hu, L.T. & Bentler, P.M. (1999) Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives. *Structural Equation Modeling: A Multidisciplinary Journal*, 6, 1–55.
- Jacques, B.J., Akahane, S., Abe, M., Middleton, W., Hoback, W.W. & Shaffer, J.J. (2009) Temperature and food availability differentially affect the production of antimicrobial compounds in oral secretions produced by two species of burying beetle. *Journal of Chemical Ecology*, 35, 871–877.
- Janzen, D.H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, 54, 687–708.
- Kline, R.B. (2010) *Principles and practice of structural equation modeling*. Guilford Press, New York, USA.
- Lee, E.-D., Min, H.-K., Oh, K.-S., Jeong, J.-C. & Cho, Y.-B. (2012) Appearance of carrion beetles (Coleoptera: Silphidae) by altitudes in Deogyusan National Park, Jeollabuk-do, Korea. *Journal of Korean Nature*, 5, 11–15.
- Lobo, J.M. & Halffter, G. (2000) Biogeographical and ecological factors affecting the elevational variation of mountainous communities of coprophagous beetles (Coleoptera: Scarabaeoidea): a comparative study. *Annals of the Entomological Society of America*, 93, 115–126.
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* 10, 3–13.
- Lumpkin, B.C. (1971) Elevational studies of Silphidae (Insecta: Coleoptera) in southeast Tennessee. Masters thesis, University of Tennessee, Knoxville, Knoxville, TN, USA.
- Martin, S. (1989) Altitudinal distribution of burying beetles (Coleoptera, Silphidae) in the Southern Alps of Japan. *Japanese Journal of Entomology*, 57, 876–879.
- May, R.M. (1988) How many species are there on earth? *Science*, 241, 1441–1449.
- McCain, C.M. (2007) Area and mammalian elevational diversity. *Ecology*, 88, 76–86.
- McCain, C.M. (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346–360.
- McCain, C.M. & Grytnes, J.-A. (2010) Elevational gradients in species richness. In: *Encyclopedia of Life Sciences (ELS)*. John Wiley & Sons, Ltd., Chichester, UK.
- McCain, C.M., King, S.R.B., Szewczyk, T. & Beck, J. (2018) Small mammal species richness is directly linked to regional productivity, but decoupled from food resources, abundance, or habitat complexity. *Journal of Biogeography*, 45, 2533–2545.
- McCoy, E.D. (1990) The distribution of insects along elevational gradients. *Oikos*, 58, 313–322.
- Merrick, M.J. & Smith, R.J. (2004) Temperature regulation in burying beetles (*Nicrophorus* spp.: Coleoptera: Silphidae): effects of body size, morphology and environmental temperature. *Journal of Experimental Biology*, 207, 723–733.

- Monteith, G.B. (1985) Altitudinal transect studies at the Cape Tribulation, North Queensland VII. Coleoptera and Hemiptera (Insecta). The Queensland Naturalist, 26, 70–80.
- Nichols, J.D. & Conroy, M.J. (1996) Estimation of species richness. In: Measuring and monitoring biological diversity: standard methods for mammals (ed. by D.E. Wilson, F.R. Cole, J.D. Nichols, R. Rudran and M.S. Foster), pp. 226–234. Smithsonian Institution Press, Washington, DC, USA.
- Nilsson, A.N. & Persson, S. (1993) Taxonomy, distribution and habitats of the Dytiscidae (Coleoptera) of Ethiopia. Entomologica Fennica, 4, 57–94.
- Olson, D.M. (1994) The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. Journal of Tropical Ecology, 10, 129–150.
- Peck, S.B. & Kaulbars, M.M. (1987) A synopsis of the distribution and bionomics of the carrion beetles (Coleoptera: Silphidae) of the conterminous United States. Proceedings of the Entomological Society of Ontario, 118, 47–81.
- Peck, S.B. & Miller, S.E. (1993) A catalog of the coleoptera of America north of Mexico. Family: Silphidae. Agriculture Handbook Number 529–28. United States Department of Agriculture.
- Prevedello, J.A., Dickman, C.R., Vieira, M.V. & Vieira, E.M. (2013) Population responses of small mammals to food supply and predators: a global meta-analysis. Journal of Animal Ecology, 82, 927–936.
- Ratcliffe, B.C. (1996) The carrion beetles (Coleoptera: Silphidae) of Nebraska. Bulletin of the University of Nebraska State Museum, 13, 1–107.
- Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. Journal of Mammalogy, 73, 715–730.
- Rosseel, Y. (2012) lavaan: an R package for structural equation modeling. Journal of Statistical Software, 48, 1–36.
- Running, S.W., Nemani, R.R., Heinsch, F.A., Zhao, M., Reeves, M. & Hashimoto, H. (2004) A continuous satellite-derived measure of global terrestrial primary production. BioScience, 54, 547–560.
- Sanders, N.J., Dunn, R.R., Fitzpatrick, M.C., Carlton, C.E., Pogue, M.R., Parker, C.R. & Simons, T.R. (2010) Diverse elevational diversity gradients in Great Smoky Mountains National Park, USA. In: Data mining for global trends in mountain biodiversity (ed. by E.M. Spehn & C. Körner), pp. 75–87. CRC Press, Boca Raton, FL, USA.
- Santos, S.M., Carvalho, F. & Mira, A. (2011) How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. PLoS ONE, 6, e25383.
- Schermelleh-Engel, K., Moosbrugger, H. & Müller, H. (2003) Evaluating the fit of structural equation models: tests of significance and descriptive goodness-of-fit measures. Methods of Psychological Research Online, 8, 23–74.
- Scott, M.P. (1994) Competition with flies promotes communal breeding in the burying beetle, *Nicrophorus tomentosus*. Behavioral Ecology and Sociobiology, 34, 367–373.
- Scott, M.P. (1996) Communal breeding in burying beetles. American Scientist, 84, 376.
- Shipley, B. (2000) Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge, UK.
- Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. Ecology, 90, 363–368.
- Slade, N.A. & Blair, S.M. (2000) An empirical test of using counts of individuals captured as indices of population size. Journal of Mammalogy, 81, 1035–1045.
- Smith, R.J. & Heese, B. (1995) Carcass selection in a high altitude population of the Burying beetle, *Nicrophorus investigator* (Silphidae). The Southwestern Naturalist, 40, 50–55.
- Stapp, P. (1997) Microhabitat use and community structure of darkling beetles (Coleoptera: Tenebrionidae) in shortgrass prairie: effects of season, shrub and soil type. The American Midland Naturalist, 137, 298–311.
- Staunton, K.M., Nakamura, A., Burwell, C.J., Robson, S.K.A. & Williams, S.E. (2016) Elevational distribution of flightless ground beetles in the tropical rainforests of north-eastern Australia. PLoS ONE, 11, e0155826.
- Storch, D., Bohdalková, E., Okie, J. & Gravel, D. (2018) The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. Ecology Letters, 21, 920–937.

- Stork, N.E., McBroom, J., Gely, C. & Hamilton, A.J. (2015) New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences USA*, 112, 7519–7523.
- Szewczyk, T. & McCain, C.M. (2016) A systematic review of global drivers of ant elevational diversity. *PLoS ONE*, 11, e0155404.
- Trumbo, S.T. (1994) Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. *Oikos*, 69, 241–249.
- Vagle, G.L. & McCain, C.M. (2020) Natural population variability may be masking the more-individuals hypothesis. *Ecology*, 101, e03035.
- Werenkraut, V. & Ruggiero, A. (2011) Quality of basic data and method to identify shape affect richness–altitude relationships in meta-analysis. *Ecology*, 92, 253–260.
- Werenkraut, V. & Ruggiero, A. (2014) The richness and abundance of epigaeic mountain beetles in north-western Patagonia, Argentina: assessment of patterns and environmental correlates. *Journal of Biogeography*, 41, 561–573.
- Wilson, D.E., Cole, F.R., Nichils, J.D., Rudran, R. & Foster, M.S. (1996) Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian, Washington, D.C., USA.
- Wolda, H., O'Brien, C.W. & Stockwell, H.P. (1998) Weevil diversity and seasonality in tropical Panama as deduced from light-trap catches (Coleoptera: Curculionoidea). *Smithsonian Contributions to Zoology*, 590, 1–79.
- Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, 41, 496–506.
- Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. In: *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 66–74. University of Chicago Press, Chicago, IL, USA.

Submitted: 18 February 2020

First decision: 23 March 2020

Accepted: 27 August 2020

Edited by Joaquín Hortal, Nagore Medina and Robert J. Whittaker