Reports

Testing the role of body size and litter depth on invertebrate diversity across six forests in North America

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Abstract. Ecologists search for rules by which traits dictate the abundance and distribution of species. Here we search for rules that apply across three common taxa of litter invertebrates in six North American forests from Panama to Oregon. We use image analysis to quantify the abundance and body size distributions of mites, springtails, and spiders in 21 1-m^2 plots per forest. We contrast three hypotheses: two of which focus on trait–abundance relationships and a third linking abundance to species richness. Despite three orders of magnitude variation in size, the predicted negative relationship between mean body size and abundance per area occurred in only 18% of cases, never for large bodied taxa like spiders. We likewise found only 18% of tests supported our prediction that increasing litter depth allows for high abundance; two-thirds of which occurred at a single deciduous forest in Massachusetts. In contrast, invertebrate abundance constrained species richness 76% of the time. Our results suggest that body size and habitat volume in brown food webs are rarely good predictors of variation in abundance, but that variation in diversity is generally well predicted by abundance.

Key words: abundance; body size; diversity; litter depth; LTER; richness.

Introduction

The abundance and richness of species varies across ecological space and through evolutionary time. Understanding why and how these two components of diversity change has long been a core objective for ecologists (MacArthur 1965, Ricklefs and Schluter 1993, Rosenzweig 1995). Numerous hypotheses about spatial and temporal drivers of diversity have been proposed throughout the years (Pianka 1966, Tilman 1987, Cardinale et al. 2004). Yet in some systems like brown food webs (i.e., detritus, decomposers, and their consumers; Kaspari and Yanoviak 2009), where an assortment of heterogeneous nutrients and structure support one of the most diverse biotas on earth (Wardle 2002), questions remain about how so many species can coexist without biotic mechanisms reducing diversity (Anderson 1975). Here we focus our efforts on two potential drivers

of diversity in brown food webs—body size and litter depth—and test hypotheses on how these drivers shape patterns of abundance and richness in litter taxa across six forests in North America.

The range of body sizes among animals spans more than 21 orders of magnitude (Smith and Lyons 2013). From the tiny crustacean, *Stygotantulus stocki* (<0.1 mm), to the colossal squid, *Mesonychoteuthis hamiltoni* (>12 m), invertebrates occupy a large portion of this size range and can increase throughout their ontogeny 4,000-fold (Klok and Chown 1999). It should not be surprising, thus, that size plays an integral role in determining an organism's temporal and spatial scale of operation (Peters 1983). Size, however, also underlies trade-offs as the demand for resources and habitat increases with body mass (Brown 1995, Rosenzweig 1995). Body size can determine and limit traits and aspects of an organism's lift history such as abundance, fecundity, foraging, metabolism, range size, and trophic position (Brown et al. 2004, Ernest 2005, White et al. 2007, Roeder and Kaspari 2017). A large effort has focused specifically on disentangling size–abundance relationships as they represent a link between an

individual's traits and the structure of the community within which that individual resides (Blackburn et al. 1993, Russo et al. 2003, Ernest 2005, White et al. 2007). We propose two hypotheses below that focus on ways in which either body size or litter depth regulate the abundance of litter invertebrates.

The body size–abundance hypothesis posits that the number of individuals of a certain taxon is constrained by the average body size of that taxon. Within a given area, there often resides a finite amount of resources which limits growth (Tilman 1982, Chase and Leibold 2003). When organisms are small, these resources can be divided among a large number of individuals. Conversely, when organisms grow and monopolize larger amounts of the resource pool, habitats consequently support fewer individuals. While this relationship may not be linear as metabolism, or the biological processing of energy, with a scaling relationship 3/4 power of body mass (Peters 1983, Brown et al. 2004), we nonetheless predict that body size, indirectly through resource use, regulates abundance.

The litter depth–abundance hypothesis posits that a taxon's abundance is constrained by the size of the habitat in which it lives. Leaf litter is a complex substrate that, up to this point, has rarely been quantitatively indexed according to its habitat variety. For soil organisms, leaf litter qualifies as a resource because it contributes to the growth rate of the consumer population and is consumed, however, it is also the habitat because its complex three-dimensional structuring offers a number of potential niche axes to partition (Hansen and Coleman 1998, Wardle 2002, Wagner et al. 2003). Moreover, leaf litter can vary 16-fold in depth at the 1-m^2 level across forest stands in Panama and Peru, creating a variety of habitats on which invertebrates can specialize (Kaspari and Yanoviak 2008). If resource availability is limited by the volume of the habitat (i.e., litter depth) and more resources can support more individuals, we predict that larger habitats should support more individuals.

Species richness represents another important property of communities that changes from place to place across the globe (Brown 1995, Rosenzweig 1995). In speciose locales, much debate has arisen on the abiotic and biotic constraints that determine the number of species (Hutchinson 1961, Anderson 1975, Wardle 2002). One such constraint is the amount of available energy within a system: the more-individuals hypothesis or MIH (Wright 1983, Currie 1991, Storch et al. 2018). The MIH posits that energy, often reported as net primary productivity or NPP, limits the number of individuals that an ecosystem can support. As populations require a certain quantity of individuals to remain viable, the number of species is consequently limited by abundance. Abundance can therefore constrain another property of taxocenes—their species richness.

While tests of the MIH are often performed across geographically defined gradients of productivity, here we test if abundance–richness relationships exist at a smaller spatial grain that is more appropriately scaled to our taxa of interest. Leaf litter systems are notoriously patchy (Yanoviak and Kaspari 2000, Wardle 2002, Richardson et al. 2018) and there has been little systematic study of the role of body size and litter depth in generating this community-level patchiness. Moreover, litter communities are composed of a diversity of orders (Hättenschwiler et al. 2005, Kaspari and Yanoviak 2009, Clay et al. 2014). Using six surveys from alpine coniferous forests to tropical rainforests, we test the generality of the MIH alone and in conjunction with our two abundance hypotheses to quantify the effects of body size and litter depth on the abundance and richness of leaf litter invertebrates.

METHODS

Study sites

Samples were collected from six forests in North America: Andrews LTER, Oregon (AND); Barro Colorado Island, Panama (BCI); Coweeta LTER, North Carolina (CWT); Harvard Forest LTER, Massachusetts (HFR); Luquillo LTER, Puerto Rico (LUQ); and Niwot Ridge LTER, Colorado (NWT). These sites vary in type from tropical rainforest (BCI, LUQ) to temperate deciduous (CWT, HFR) or coniferous forests (AND, NWT) across approximately 35° of latitude (Appendix S1: Fig. S1). At each site, 21 1-m^2 plots were arrayed in a cross design with plots placed 1, 10, 50, 100, and 200 m at each cardinal direction from a central plot (Weiser et al. 2018).

Invertebrate sampling

Invertebrates were collected from each plot by sifting litter and approximately 0.5 cm of mineral soil through 1-cm mesh screens. Invertebrates were then extracted from the siftate over 48 h in Tulgren funnels with 25 W bulbs (Weiser et al. 2018). Individuals were sorted taxonomically, counted, and assigned to morphospecies, which often represents a reliable estimate of species richness for invertebrate community analyses (Oliver and Beattie 1996). Mites (Acari), springtails (Collembola), and spiders (Arachnida) were the most abundant invertebrate groups collected within most plots and we focus on differences amongst these three groups for our analyses.

Body size and litter depth measurements

For each plot, all individuals from the three focal groups listed above were photographed within a 10 × 10 mm box set at 10× magnification using a Leica EC3 digital camera with FireCam software version 3.4.1 (Leica Microsystems, Wetzlar, Germany) mounted on a Leica S8 APO stereo microscope. After photos were cropped and resized using Adobe Photoshop CS3 version 10.0.1 (Adobe Systems, San Jose, California, USA),

the length and width of each individual, representing the major and minor axes respectively, were measured in mm using ImageJ (U.S. National Institutes of Health, Bethesda, Maryland, USA). As the body shape of most invertebrates roughly resembles an ellipse, which may be a better correlate of size (i.e., mass), we also calculated ellipse area using the equation: area = $\pi \times$ (length/2) $\times$ (width/2). To validate our methods, digital measurements from a subset of mites were compared to those from an ocular micrometer and found to be similar (Appendix S1: Fig. S2; $r = 0.998$, $P < 0.0001$). We then dried 84 of those mites to constant mass at 60°C for 48 h and weighed them to the nearest 0.001 mg on a Cahn microbalance (Cahn Instruments, Cerritos, California, USA). Of the three body size measurements, ellipse area was the best correlate to mass (Appendix S1: Fig. S3; $r = 0.940$, $P < 0.0001$) and subsequently used in all hypothesis tests. Litter depth, our measure of habit size for invertebrates, was measured 1 cm from the four corners of each plot and averaged. We exclude two plots from our analysis, one at AND due to litter depth not being recorded and the second at NWT due to the absence of any individual from our selected taxa. This changes the total number of potential plots used to 124. Of those 124 plots, invertebrates were available for measurement in 123, 102, and 78 plots for mites, springtails, and spiders, respectively.

Statistics for hypothesis testing

Analyses were run in R version 3.5.1 (R Core Team 2018). All variables. were $\log_{10}$-transformed to meet the assumptions of normality. Predictor variables in multiple regression models were checked for multicollinearity using a variance inflation factor (VIF) cutoff = 3 in the car package (Fox and Weisberg 2019). We focus on patterns of abundance and richness within sites, replicating analyses for each location ($N = 6$) and taxonomic group ($N = 3$) to determine the generality of our results.

Abundance.— To test the body size–abundance and litter depth–abundance hypotheses, we used ordinary least squares (OLS) regression in an information theoretic approach to rank all possible regression models by Akaike's information criterion corrected for small sample size (AIC_c). ΔAIC_c values for each model were calculated from the difference of the AIC_c of the ith model and the model with the lowest AIC_c value. Akaike weights (w_i) were then calculated and represent a weight of evidence that model i was the best fit. AIC_c and Akaike weights (w_i) were calculated in the MuMIn and qpcR packages. We test the prediction that a smaller mean body size results in more individuals being supported within a given area and that deeper litter (i.e., more habitat) resulted in more individuals being supported. While we propose hypothetical reasons for why both body size and litter depth could individually affect abundance, we also test for interactions between these

two variables as both may be working together to drive patterns of abundance.

Richness.— To test the more-individuals hypothesis, we used OLS regressions to compare abundance to species richness across plots within sites.

RESULTS

Across six forests in North America, we collected 46,762 mites, springtails, and spiders that varied in size across three orders of magnitude. These focal taxa were patchily distributed at the 1-m^2 scale, yet much of that patchiness could be found in any given forest. Tropical rainforests and temperate deciduous forests supported a larger variety of body sizes (CV; BCI = 2.66, CWT = 3.59, HFR = 3.37, LUQ = 3.26) than temperate coniferous forests (CV; AND = 1.16, NWT = 0.77). However, this was often dependent on the taxonomic group (Appendix S1: Fig. S4). Litter depth varied less within sites (CV: AND = 0.31, BCI = 0.51, CWT = 0.38, HFR = 0.54, LUQ = 0.36, NWT = 0.44) but a 3.3-fold difference in mean values was still observed across sites (Appendix S1: Fig. S5) as deep litter banks were maintained at locations like AND (mean = 11.9 cm) and CWT (mean = 12.2 cm) compared to HFR (mean = 3.7 cm) or LUQ (mean = 5.3 cm).

Testing body size and litter depth–abundance hypotheses

The predicted negative relationship between mean body size and abundance per area was observed in two of the six sites for mites, one of the six sites for springtails, and in none of the sites for spiders (Table 1). Similarly, the predicted increase in abundance as litter depth increased was found in one site each for mites, springtails, and spiders (Table 1). Although we occasionally found competing models that contained the combination of body size and litter depth as the top model or within <2 AIC_c of the top model, there was no evidence of interaction between these two drivers (i.e., interaction models were always >2 AIC_c of the top model).

Testing the more-individuals hypothesis

We found stronger support for the more-individuals hypothesis, as it was significant in 13 of the 17 (76%) taxa by site combinations we tested (Fig. 1; Appendix S1: Table S1). For mites, richness per area increased with abundance per area at four of the six sites (AND, BCI, CWT, NWT) with abundance accounting for 54–79% of the variation in species richness ($P < 0.001$; Fig. 1a). Similarly, at every location besides NWT ($P = 0.088$), 30–81% of the species richness of springtails was accounted for by abundance ($P < 0.05$; Fig. 1b). All abundance–richness relationships for spiders except CWT ($P = 0.064$) were significant ($P < 0.05$,

TABLE 1. AIC$_c$ scores and weights of top multiple linear regression models for body size (BS) or litter depth (LD) and abundance.

Taxon and site	Model	Intercept	BS	LD	AIC$_c$	ΔAIC$_c$	w_i	r^2
Mites								
AND	BS	1.16	−1.18	–	−6.90	0.00	0.79	0.47
BCI	BS	0.27	−1.94	–	15.52	0.00	0.67	0.34
BCI	BS + LD	0.06	−1.91	0.33	17.51	1.99	0.25	0.34
CWT	BS + LD	−0.52	−1.81	1.16	22.90	0.00	0.42	0.29
CWT	LD	1.05	–	1.19	23.26	0.36	0.35	0.20
HFR	null	2.90	–	–	1.95	0.00	0.33	–
LUQ	null	2.25	–	–	19.61	0.00	0.40	–
NWT	null	2.09	–	–	43.40	1.44	0.24	–
Springtails								
AND	null	1.09	–	–	35.01	0.00	0.30	–
BCI	null	1.15	–	–	22.39	0.00	0.63	–
CWT	null	1.64	–	–	16.40	0.19	0.39	–
HFR	LD	0.53	–	1.64	39.36	0.00	0.30	0.25
HFR	BS + LD	0.24	−0.81	1.12	39.48	0.12	0.29	0.32
HFR	BS	0.55	−1.21	–	39.54	0.18	0.28	0.25
LUQ	null	0.97	–	–	23.71	1.64	0.24	–
NWT	null	1.68	–	–	23.66	0.00	0.72	–
Spiders								
AND	null	0.42	–	–	9.92	0.00	0.41	–
BCI	null	0.63	–	–	8.58	1.69	0.23	–
CWT	null	1.16	–	–	−3.72	0.00	0.61	–
HFR	LD	0.57	–	0.82	−9.21	0.00	0.80	0.52
LUQ	null	0.60	–	–	16.83	0.00	0.44	–

Notes: Null models are intercept-only models and reported when they were the top model or within 2 ΔAIC$_c$ of the top model. No spiders were collected at NWT. Sites are identified in *Methods: Study sites.* –, null value.

$r^2 = 0.33–0.75$), despite the fact that spiders occurred in fewer plots on average (Fig. 1c).

DISCUSSION

Our body size and litter depth–abundance hypotheses assume that resources in the litter (e.g., food, predator-free space) are important constraints to the fitness of taxa. Yet despite three orders of magnitude variation in body size and a 3.3-fold variation in litter volume across a range of forest types, we generally found weak and inconsistent support for either of these models (~18%), especially in the largest taxa—spiders. In contrast, abundance itself regularly constrains species richness (~76% of all models with an alpha level of 0.05). Why, though, was plot diversity easier to predict than plot abundance for these three common litter taxa?

Although we had only modest success predicting patterns of abundance, abundance itself was a strong and consistent predictor of a plot's species richness of mites, springtails, and spiders (Fig. 1). We posit one reason that such strong patterns occur is due to the intrinsic nature of how species richness scales with abundance—there cannot be more species than individuals in a given unit of area. But we note that, while model intercepts for spiders routinely approached unity (Appendix S1: Table S1), those of springtails and mites did not. The more-individuals hypothesis, thus, can be a powerful shortcut toward predicting differences in plot richness of taxonomically challenging organisms through the relatively simple exercise of counting them.

In contrast—and despite 225-, 292-, and 34-fold variation in abundance per area for mites, springtails, and spiders—two candidates for drivers of this variation were successful in only 18% of tests. The logic of body size is clear: larger organisms need more space and resources (Damuth 1987, Cyr et al. 1997). But there is growing evidence that this pattern breaks down at smaller grains of observation (Blackburn et al. 1993, White et al. 2007). One way this may arise is if sampling at small spatial scales constrains the number of individuals sampled and hence the power of the analysis. For example, mites and springtails comprise up to 95% of the total number of microarthropods in many ecosystems (Seastedt 1984, Bardgett and Cook 1998). Spiders, in comparison, make up only a fraction of the abundance of these groups and are often more patchily distributed (Uetz 1975). We observed such discrepancies in abundance for our measured taxa as we recorded 64-fold more mites (abundance = 41,877) and sixfold more springtails (abundance = 4,229) than spiders (abundance = 656). Consequently, variation in spider body size from plot to plot might be incredibly high as single individuals that are either very large or very small can have a big impact due to the low abundance of that taxon (average spider abundance per plot = 8.4). However, mites were readily
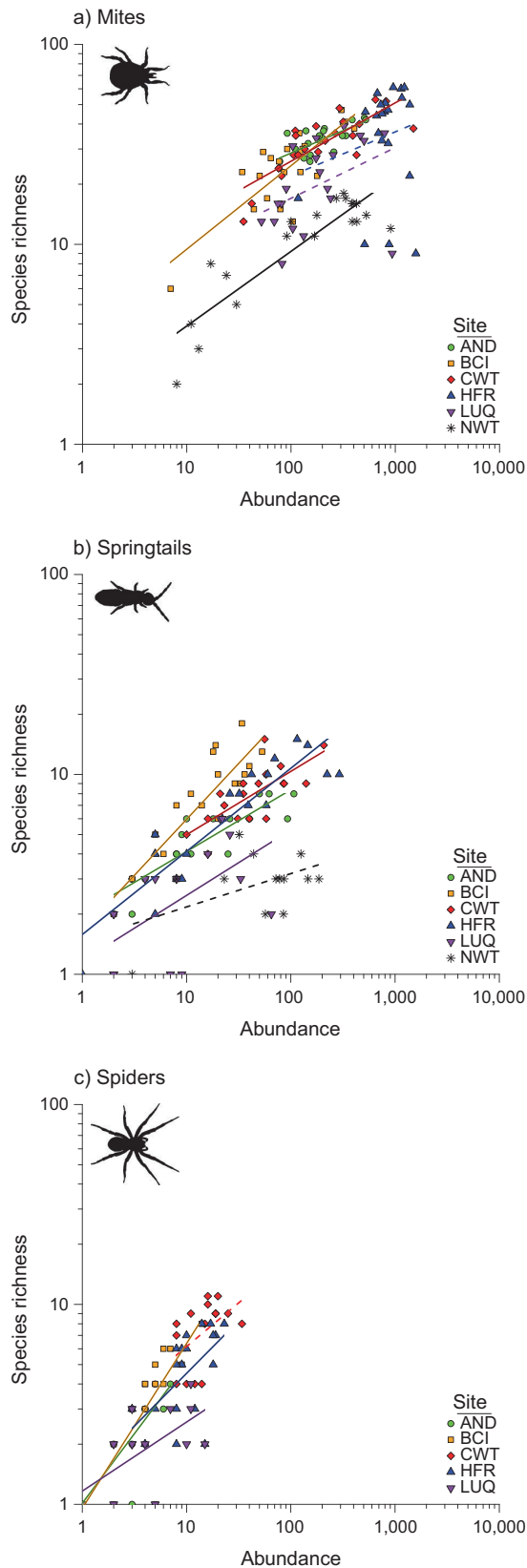
a) Mites

b) Springtails

c) Spiders

Fig. 1. Abundance–richness relationships testing the

(Fig. 1. *Continued*)
more-individuals hypothesis (MIH) across three taxa and six sites in North America. Significant relationships ($P \leq 0.05$) are represented by solid colored lines, while dashed lines represent nonsignificant relationships. Model outputs can be found in Appendix S1: Table S1. Sites are identified in *Methods: Study sites*.

abundant (average mite abundance per plot = 340.5) and mean plot values were less impacted by single individuals. If size–abundance relationships only become apparent when a certain number of individuals are present, then there may have not been enough statistical power to detect body size effects.

Likewise, habitat volume—effective in predicting patterns of abundance at larger scales (Post et al. 2000)—only accounted for variation in abundance in three of our single-parameter models, two of which occurred at HFR. As we suggest for body size, one reason may be statistical: litter depth at HFR had the highest coefficient of variation across plots (CV = 0.54) and thus provided the greatest range of litter depths from which to detect a pattern. A second possibility is that litter depth is not necessarily linearly associated with food supply. If decomposition is the engine in which leaves and pine needles are converted into microbial biomass and hence fuel for the brown food web (Shik and Kaspari 2010), forests with deep litter like CWT (Mean = 12.2 cm) may be rotting more slowly and hence producing less food per area compared to the shallow, variable litter of HFR (mean = 3.7 cm).

CONCLUSIONS

Two models of abundance, firmly rooted in the hypothesis that consumers accumulate in patches relative to their metabolic rate and food supply, were effective in 6 of 34 cases for common taxa of forest brown food webs. Understanding variation of forest litter invertebrates is surprisingly challenging as the system appears to be highly dynamic and non-equilibrial with a multitude of processes at small spatial grains swamping the role of per capita resource requirements (Gaston et al. 2008, Chown and Gaston 2010). We suggest two working hypotheses.

First, mean annual temperature ranged from 2.5° to 25.7°C, a 10.3-fold difference, across our six sites. The abiotic conditions of cold locales may have additional constraints on size or abundance that limited the utility of our hypotheses. In rodents, for example, the distribution of body sizes was recently found to be more similar across species at sites with lower minimum temperatures (Read et al. 2018). Thus, body size and litter depth may fail to predict abundance at locations that are abiotically challenging like NWT in Colorado, which had the coldest mean temperature and low but similar coefficients of variation in size for mites (CV = 0.77) and springtails (CV = 0.78).

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Second, mites, springtails, and spiders make up a portion of leaf litter communities that are fluid in time. Our tacit assumption is that abundance per area is fixed, yet this is rarely the case as predacious spiders can be highly mobile (Clarke and Grant 1968) and disturbance by abiotic (e.g., rainfall) and biotic factors (e.g., army ant raids) can drastically change invertebrate densities. Likewise, litter depth may vary in resource supply and palatability under different tree species, resulting in patchy zones that vary in nutrient availability, moisture, and decomposition (Aerts 1997, Kaspari et al. 2008, Gora et al. 2018)—all of which may directly or indirectly affect the abundance and richness of invertebrates.

LITERATURE CITED

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449.

Anderson, J. M. 1975. The enigma of soil animal species diversity. Pages 51–58 *in* J. Vaněk, editor. Progress in soil zoology. Springer Netherlands, Dordrecht, Netherlands.

Bardgett, R. D., and R. Cook. 1998. Functional aspects of soil animal diversity in agricultural grasslands. Applied Soil Ecology 10:263–276.

Blackburn, T. M., V. K. Brown, B. M. Doube, J. D. Greenwood, J. H. Lawton, and N. G. Stork. 1993. The relationship between abundance and body size in natural animal assemblages. Journal of Animal Ecology 62:519–528.

Brown, J. H. 1995. Macroecology. The University of Chicago Press, Chicago, Illinois, USA.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Cardinale, B. J., A. R. Ives, and O. Inchausti. 2004. Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. Oikos 104:437–450.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. The University of Chicago Press, Chicago, Illinois, USA.

Chown, S. L., and K. J. Gaston. 2010. Body size variation in insects: a macroecological perspective. Biological Reviews 85:139–169.

Clarke, R. D., and P. R. Grant. 1968. An experimental study of the role of spiders as predators in a forest litter community. Part 1. Ecology 49:1152–1154.

Clay, N. A., S. P. Yanoviak, and M. Kaspari. 2014. Short-term sodium inputs attract microbe-detritivores and their predators. Soil Biology and Biochemistry 75:248–253.

Currie, D. 1991. Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137:27–49.

Cyr, H., R. H. Peters, J. A. Downing, and H. Cyr. 1997. Population density and community size structure: comparison of aquatic and terrestrial systems. Oikos 80:139–149.

Damuth, J. 1987. Interspecific allometry of population-density in mammals and other animals—the independence of body-mass and population energy-use. Biological Journal of the Linnean Society 31:193–246.

Ernest, S. K. M. 2005. Body size, energy use, and community structure of small mammals. Ecology 86:1407–1413.

Fox, J., and Weisberg, S. 2019. An R companion to applied regression. Third Edition. Sage, Thousand Oaks, California, USA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gaston, K. J., S. L. Chown, and K. L. Evans. 2008. Ecogeographical rules: elements of a synthesis. Journal of Biogeography 35:483–500.

Gora, E. M., E. J. Sayer, B. L. Turner, and E. V. J. Tanner. 2018. Decomposition of coarse woody debris in a long-term litter manipulation experiment: a focus on nutrient availability. Functional Ecology 33:1128–1138.

Hansen, R. A., and D. C. Coleman. 1998. Litter complexity and composition are determinants of the diversity and composition of oribatid mites (Acari: Oribatida) in litterbags. Applied Soil Ecology 9:17–23.

Hättenschwiler, S., A. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystem. Annual Review of Ecology, Evolution, and Systematics 36:191–218.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist 95:137–145.

Kaspari, M., M. N. Garcia, K. Harms, M. Santana, S. J. Wright, and J. B. Yavitt. 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecology Letters 11:35–43.

Kaspari, M., and S. P. Yanoviak. 2008. Biogeography of litter depth in tropical forests: evaluating the phosphorus growth rate hypothesis. Functional Ecology 22:919–923.

Kaspari, M., and S. P. Yanoviak. 2009. Biogeochemistry and the structure of tropical brown food webs. Ecology 90:3342–3351.

Klok, C. J., and S. L. Chown. 1999. Assessing the benefits of aggregation: thermal biology and water relations of anomalous Emperor Moth caterpillars. Functional Ecology 13:417–427.

MacArthur, R. H. 1965. Patterns of species diversity. Biological Reviews 40:510–533.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology 10:99–109.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. American Naturalist 100:33–46.

Post, D. M., M. L. Pace, and N. G. Hairston Jr. 2000. Ecosystem size determines food-chain length in lakes. Nature 405:1047–1049.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Read, Q. D., J. M. Grady, P. L. Zarnetske, S. Record, B. Baiser, J. Belmaker, M. Tuanmu, A. Strecker, L. Beaudrot, and K. M. Thibault. 2018. Among-species overlap in rodent body size distributions predicts species richness along a temperature gradient. Ecography 41:1718–1727.

Richardson, B. A., M. J. Richardson, and F. M. Soto-Adames. 2018. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. Journal of Animal Ecology 74:926–936.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity: regional and historical influences. The University Press of Chicago, Chicago, Illinois, USA.

Roeder, K. A., B. R. Benson, M. D. Weiser, and M. Kaspari. 2021. Data from: Testing the role of body size and litter depth on invertebrate diversity across six forests in North America. Ag Data Commons. https://doi.org/10.15482/USDA.ADC/1524261

Roeder, K. A., and M. Kaspari. 2017. From cryptic herbivore to predator: stable isotopes reveal consistent variability in trophic levels in an ant population. Ecology 98:297–303.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Russo, S. E., S. K. Robinson, and J. Terborgh. 2003. Size-abundance relationships in an Amazonian bird community: implications for the energetic equivalence rule. American Naturalist 161:267–283.

Seastedt, T. R. 1984. The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29:25–46.

Shik, J. Z., and M. Kaspari. 2010. More food, less habitat: how necromass and leaf litter decomposition combine to regulate a litter ant community. Ecological Entomology 35:158–165.

Smith, F. A., and S. K. Lyons. 2013. Animal Body Size: Linking pattern and process across space, time, and taxonomic group. The University Press of Chicago, Chicago, Illinois, USA.

Storch, D., E. Bohdalková, and J. Okie. 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.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57:189–214.

Uetz, G. W. 1975. Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. Environmental Entomology 4:719–724.

Wagner, J. D., S. Toft, and D. H. Wise. 2003. Spatial stratification in litter depth by forest-floor spiders. Journal of Arachnology 31:28–39.

Wardle, D. A. 2002. Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton, New Jersey, USA.

Weiser, M. D., S. T. Michaletz, V. Buzzard, Y. Deng, Z. He, L. Shen, B. J. Enquist, R. B. Waide, J. Zhou, and M. Kaspari. 2018. Toward a theory for diversity gradients: the abundance-adaptation hypothesis. Ecography 41:255–264.

White, E. P., S. J. M. Ernesst, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in Ecology and Evolution 22:323–330.

Wright, D. 1983. Species-energy theory: an extension of species-area theory. Oikos 41:496–506.

Yanoviak, S. P., and M. Kaspari. 2000. Community structure and the habitat template: ants in the tropical forest canopy and litter. Oikos 89:259–266.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3601/suppinfo

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Data (Roeder et al. 2021) are available from USDA's Ag Data Commons at https://doi.org/10.15482/USDA.ADC/1524261

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