

## Resolving the roles of body size and species identity in driving functional diversity

Volker H. W. Rudolf, Nick L. Rasmussen, Christopher J. Dibble and Benjamin G. Van Allen

*Proc. R. Soc. B* 2014 **281**, 20133203, published 5 March 2014

---

### Supplementary data

["Data Supplement"](#)

<http://rspb.royalsocietypublishing.org/content/suppl/2014/03/04/rspb.2013.3203.DC1.html>

### References

[This article cites 44 articles, 6 of which can be accessed free](#)

<http://rspb.royalsocietypublishing.org/content/281/1781/20133203.full.html#ref-list-1>

### Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (1791 articles)

### Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)



## Research

**Cite this article:** Rudolf VHW, Rasmussen NL, Dibble CJ, Van Allen BG. 2014 Resolving the roles of body size and species identity in driving functional diversity. *Proc. R. Soc. B* **281**: 20133203.  
<http://dx.doi.org/10.1098/rspb.2013.3203>

Received: 6 December 2013

Accepted: 3 February 2014

### Subject Areas:

ecology

### Keywords:

size spectra, allometry, food web, ontogenetic niche shift, trophic cascade, functional diversity

### Author for correspondence:

Volker H. W. Rudolf

e-mail: [volker.rudolf@rice.edu](mailto:volker.rudolf@rice.edu)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2013.3203> or via <http://rspb.royalsocietypublishing.org>.

# Resolving the roles of body size and species identity in driving functional diversity

Volker H. W. Rudolf, Nick L. Rasmussen, Christopher J. Dibble and Benjamin G. Van Allen

Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77005, USA

Efforts to characterize food webs have generated two influential approaches that reduce the complexity of natural communities. The traditional approach groups individuals based on their species identity, while recently developed approaches group individuals based on their body size. While each approach has provided important insights, they have largely been used in parallel in different systems. Consequently, it remains unclear how body size and species identity interact, hampering our ability to develop a more holistic framework that integrates both approaches. We address this conceptual gap by developing a framework which describes how both approaches are related to each other, revealing that both approaches share common but untested assumptions about how variation across size classes or species influences differences in ecological interactions among consumers. Using freshwater mesocosms with dragonfly larvae as predators, we then experimentally demonstrate that while body size strongly determined how predators affected communities, these size effects were species specific and frequently nonlinear, violating a key assumption underlying both size- and species-based approaches. Consequently, neither purely species- nor size-based approaches were adequate to predict functional differences among predators. Instead, functional differences emerged from the synergistic effects of body size and species identity. This clearly demonstrates the need to integrate size- and species-based approaches to predict functional diversity within communities.

## 1. Introduction

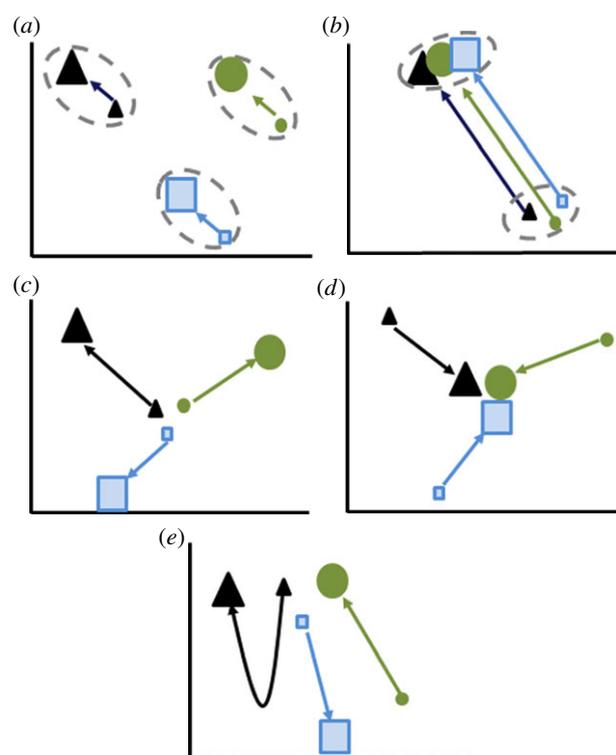
To cope with the apparent complexity of natural communities, ecology has traditionally taken a reductionist approach. For instance, in food webs, organisms are traditionally grouped into species (or trophic groups containing multiple species) based on the Linnean taxonomic system [1]. This approach, however, has several limitations. First, species identity itself cannot be used to *a priori* predict the strength and type of ecological interactions of organisms without additional information about the trait and biology of the species. Secondly, it ignores any variation in ecological interactions with species, despite the growing evidence indicating that functional differences within species can rival or even exceed differences between species [2–5].

To overcome the limitations of this ‘curse of the Latin binomial’ [6], an alternative size-based approach has been developed, which ignores the taxonomic identity of individuals and instead groups individuals by their body mass to describe the dynamics and structure of whole communities [1,7]. This size-based approach is based on empirical work demonstrating that (i) natural communities often exhibit regular size–abundance relationships (i.e. size spectra [8–12]) and (ii) body size is a key factor determining ecological interactions (e.g. who eats whom and at what rate [13–15]). Consequently, unlike species-based approaches, size-based approaches have the potential to provide a mechanistic framework to predict species interactions and community dynamics [1,14,16] but are still based on just one variable. Such a mechanistic, purely size-based approach has been successfully applied to study the structure and dynamics

of marine and some terrestrial ecosystems and guide conservation and management strategies [12,17–21].

Despite this success and rapidly increasing implementation of a size-based approach to food web ecology [1,6,16,22,23], it remains unclear how well it can explain functional differences among consumers, i.e. how consumers differ in their effect on a given community. A key assumption underlying a purely size-based approach is that differences in the direct and indirect interactions of individuals (and thus functional differences) can fully be explained by differences in the size of individuals (i.e. species identity does not matter). Yet, there is clear evidence that similar-sized individuals of different species can have different diets, even within guilds of consumers [3,24–29]. This variation among species, but within size classes, demonstrates that other species traits (e.g. morphology and behaviour) can be important for determining functional differences among consumer individuals [30]. This suggests that size and species identity are both important for determining the functional role of individuals, because knowing only the species or the size class of a given individual may not adequately describe its function in a community [3,31]. Yet, most studies (especially food web studies) to date assume that one approach or the other alone is sufficient to model the dynamics of natural communities. The extent to which size and species interact to determine differences in the ecological interactions of individuals therefore remains unclear, hampering our ability to develop a more holistic, integrative framework that accounts for both body size and species identity.

The utility of purely size- or species-based approaches not only depends on whether differences in trophic interactions are larger among size classes or species, but also on how the species interactions change with size during ontogeny. For instance, if species-specific differences in ecological interactions remain constant with change in size during ontogeny, body size and species effects are additive, and either a purely size- or species-based approach can be valid (figure 1*a* versus 1*b*). However, if differences in interactions between species change with size during ontogeny, neither approach by itself can correctly describe functional diversity (figure 1*c–e*). For instance, the diversity of resources used by individual consumers typically increases with size [31]. If the diversity of potential resources is limited for small but not large size classes, smaller size classes could be forced to use the same resources, increasing their ecological similarity. Large size classes could more effectively partition resources, reducing functional overlap (i.e. increasing dissimilarity) in ecological interactions among species with increasing size. The opposite pattern could emerge if large but not small size classes are limited by the diversity of resources (figure 1*c,d*). In other words, species identity might matter only at certain body sizes or ontogenetic stages. Alternatively, changes in the presence and strength of ecological interactions during ontogeny may be species specific and/or nonlinear, and functional differences among species could be unrelated to the size of organisms (figure 1*e*). Identifying which scenario is present in natural communities is crucial to predict how losing certain organism groups affect natural communities. For instance, if body size explains most of the functional diversity within communities, size-selective harvesting can strongly alter ecosystem functioning. However, if species diversity, not body size, determines functional diversity, size-selective harvesting may have comparatively



**Figure 1.** To determine how body size and species identity influence functional differences among consumers, we can use results from community ordination techniques (non-metric multidimensional scaling (nMDS) or PCO) summarizing the effect of individuals on a reference community. Symbols and colours represent species and arrows indicate how communities shift between the smallest and largest size class of consumers during ontogeny. For clarity, similar size ranges are shown, but the concept applies also to situations when size ranges can vary across species given that they have some overlap; in such scenarios, the beginnings, ends and length of arrows would vary across species but they would still remain parallel for (*a,b*). (*a*) Traditional taxonomic approach: differences in trophic interactions among species exceed those among size classes within species. (*b*) Purely size-based approach: differences among size classes are greater than among species. Both (*a,b*) require that relative differences across species remain constant across size or species, i.e. are additive (arrows are parallel). (*c–e*) Effects of taxonomy and body size are non-additive, and differences among species either (*c*) increase with size, (*d*) decrease with size or (*e*) show no consistent pattern. Note that differences among size classes can also be nonlinear (e.g. in panel (*e*), black triangle species).

little influence on ecosystem functioning as long as species diversity is preserved.

Here, we experimentally test, for the first time, how the effects of body size and species identity interact with each other to determine functional differences among predators within a complex aquatic community. By quantifying changes in community structure, we demonstrate that the differences in ecological interactions among predators are influenced by both size and species identity effects but that there was no consistent effect of size across species. As a consequence, body size and species identity effects were not additive, and functional differences between predators increased or decreased with size across species depending on the specific species involved. These results demonstrate that neither species-based nor purely size-based approaches are adequate to predict functional diversity in natural communities. This indicates the need of a synergistic approach that unites both body size and species identity to predict functional diversity and how ecosystems respond to community disturbance.

## 2. Material and methods

Identifying how functional differences among consumers are influenced by size and species identity is challenging in natural communities because community structure varies substantially across space and time. To limit this variation, we took an experimental approach in which we independently manipulated the body size and species identity of predators in a full factorial design, with each combination of predator species and size class introduced separately to a replicate of a complex reference community. Previous studies demonstrate that changes in community structure are directly linked to a range of ecosystem processes [2,3]. Thus, any difference in the community structure among predator treatments indicated differences in their functional roles. This allowed us to use well-developed multivariate statistics to partition the variance in community structure to identify how size and species identity interact to influence differences in direct and indirect ecological interactions (and thus functional differences) among consumers.

### (a) Focal species

We focused on a guild of larvae of three libellid dragonfly species that commonly co-occur in fishless pond communities in southeast Texas: *Erythemis simplicicollis*, *Plathemis lydia* and *Pachydiplax longipennis*. These are the most abundant species in our study sites and have highly size-structured populations. Dragonfly larvae are generalist predators that can strongly influence the composition of fishless pond communities [2,32,33]. While all three focal species are likely to overlap in their diet, they also differ to some extent in their morphology and microhabitat use; *E. simplicicollis* prefers vegetation, *P. longipennis* prefers leaf litter and *P. lydia* prefers the sediment (see the electronic supplementary material).

### (b) Experimental design

The experiment used a  $3 \times 3$  factorial design which independently manipulated the species identity (three species) and size (small (S), medium (M) and large (L)) of individual predators plus a control without a focal predator addition, resulting in 10 total treatments. Each treatment was replicated six times and arranged in a randomized complete block design. We picked the three size classes to keep the mass (and head width) of individuals within a size class as constant as possible across species, within the constraints imposed by the natural differences in body morphology (see the electronic supplementary material, table S1 for details). Because large instars were on average approximately three and approximately eight times heavier than medium and small instars across species, respectively (electronic supplementary material, table S1), we adjusted the number of individuals per mesocosm using the same ratio (three L individual, nine M or 24 S). This assured that total dragonfly biomass varied on average less than 15% across predator treatments while keeping total density constant within a size treatment across species. Individual differences among species could differ more or less because differences in morphologies of species prevent a perfect biomass match (electronic supplementary material, table S1). We found no significant difference in the proportional survival of focal predators among treatments (GLM with binomial error,  $\chi^2 = 0.509$ ,  $p > 0.999$ ). All densities are within the range observed in nature.

### (c) Experimental communities

Experiments were carried out in outdoor mesocosms consisting of 62.5-l plastic containers (L  $\times$  W  $\times$  H: 67  $\times$  41  $\times$  31 cm) filled with reconditioned tap water (to a depth of 25 cm) and approximately 2 cm of sand substrate (see the electronic supplementary material). To account for potential differences in microhabitat

use among species, we created three equally sized habitat zones that differed in vegetation and leaf litter composition within a mesocosm (see the electronic supplementary material). Complex communities were established by stocking animals from local fishless pond communities (see the electronic supplementary material). After one week of exposure to focal consumer treatments, we quantified animal biomass and community structure by collecting all animals within a mesocosm, and counting, measuring and weighing more than 36 560 individuals from 47 morphospecies covering a diverse range of taxa, functional groups and size classes (electronic supplementary material, table S2).

### (d) Statistical analysis

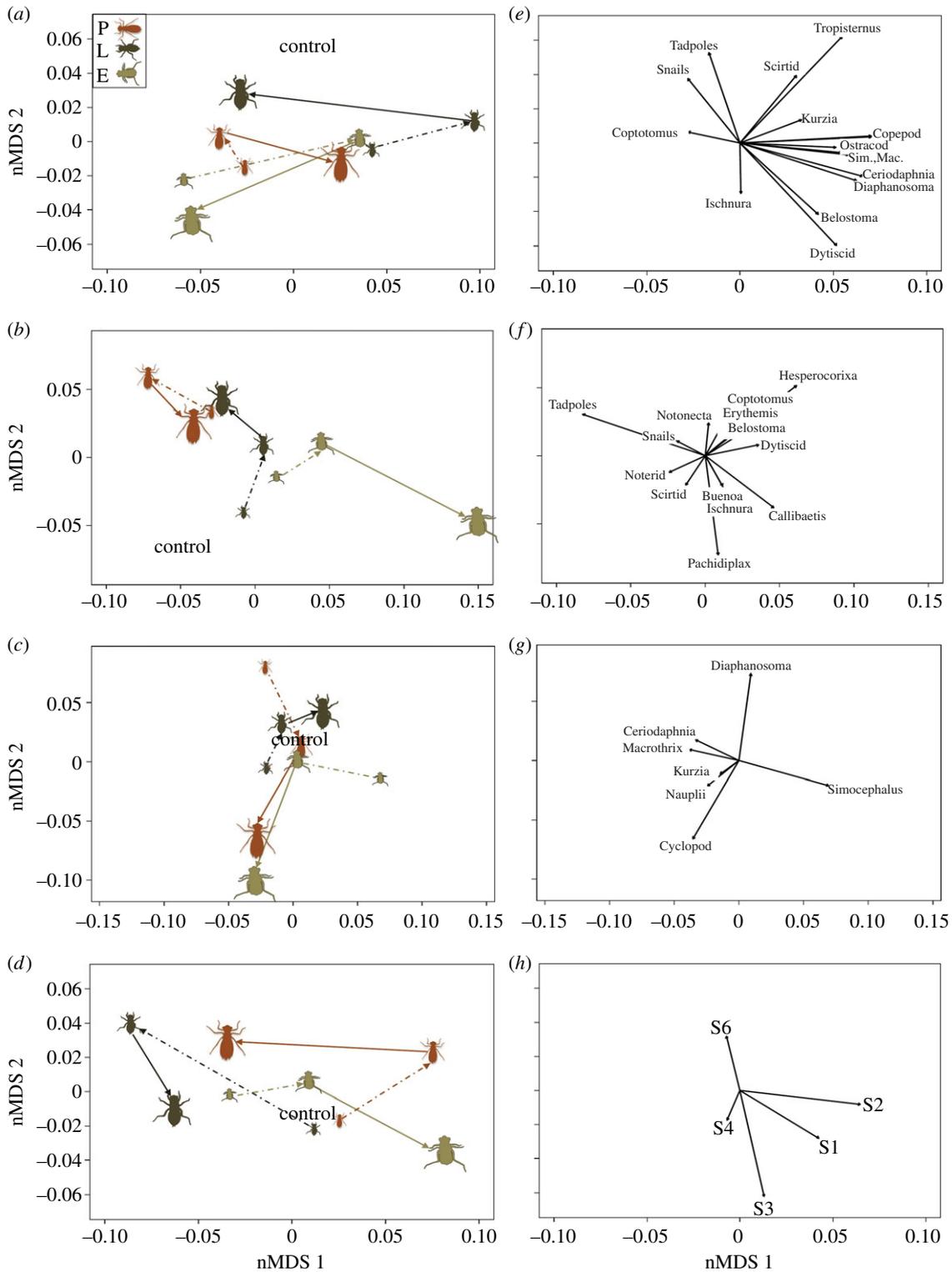
Because each of the nine predator 'groups' was allowed to interact with the same reference community, differences in the final community structure reflect all the differences among predators in the direct and indirect interactions with communities, i.e. their functional differences. We used a combination of multivariate non-parametric permutational statistics based on Bray–Curtis distances to partition the variance in community structure (see the electronic supplementary material for details) to test the hypotheses outlined in figure 1*a–e* about the relative and joint effects of size versus species identity for determining differences among predators.

First, we tested for overall differences in community structure among treatments using PERMANOVA [34,35], with size and species as fixed factors and spatial block as a random factor. If there is no significant interaction, size and species identity have independent effects, and we can partition the variance explained by each factor to determine the relative importance of factors (i.e. distinguish between figure 1*a,b*). However, a significant interaction among size and species identity treatments would indicate that size and species identity effects are not independent, i.e. functional similarity among species changes with size (figure 1*c–e*). Given a significant interaction effect, we can then determine whether functional similarity predictably scales with size (e.g. whether it increases or decreased with size; figure 1*c,d*). This was done by calculating the average distance among treatments following Huygens' theorem as  $\sqrt{(\text{sum of all squared inter-centroid distances of all species treatments within a given size class/number of species})}$ ; see the electronic supplementary material). Comparing these distances among size treatments indicates whether and how differences among species change with size. In addition, we also examined the per-biomass effect of predators on different trophic groups. To account for the small variation in initial total predator mass across treatments (electronic supplementary material, table S1), we also tested whether total predator mass was significantly related to community structure, but this was never the case (see the electronic supplementary material for details and results). A detailed description of all statistical analysis is available in the electronic supplementary material.

## 3. Results

### (a) Community structure

While specific differences among predator treatments varied depending on how community structure was analysed (figure 2*a–d*), there was one general pattern: community structure was always significantly affected by the interaction of size and species treatments (figure 2*e–h* and table 1). This clearly indicates that size and species effects were not additive, and neither one alone was sufficient to explain functional differences among predators. The interaction between size and species identity emerged because there was no consistent



**Figure 2.** Consumer effect on community structure in the experiment. Two nMDS axes of proportional (a) biomass, (b) density of macrofauna, (c) density of zooplankton species and (d) proportional abundance of different animal size classes for different predator treatments. Symbols show the average community structure (i.e. centroid) of a given treatment with size indicating the size class of a given species (P = *P. longipennis*, L = *P. lydia*, E = *E. simplicicollis*). Arrows indicate transitions between small and medium (dashed) and medium and large (solid) size classes within species. Comparison of arrows for a given size transition across species indicates how size changes influence functional differences among predator species. Panels (e–h) show the corresponding species or size class loadings for panels (a–d), with S1 indicating the smallest and S6 the largest size class. Only species with significant correlations are shown for clarity in panels (e–g). For full statistical analysis, see table 1.

effect of how changing predator size influenced community structure. Instead, the direction and magnitude of the effect of changing predator size frequently varied among species, which can easily be seen by comparing the direction and length of arrows in figure 2a–d. For instance, when

community structure was based on proportional biomass of species (figure 2a,e), increasing predator size from medium to large altered species composition, shifting the centroid of the respective treatment in the opposite direction for *P. longipennis* compared to *E. simplicicollis*, and the magnitude of this shift

**Table 1.** Effects of consumer size and species identity on community structure. Community structure was analysed with PERMANOVA and reported test statistics are pseudo- $F$  values. Community structure was analysed based on proportional biomass and abundances of species or  $\log_{10}$  size classes (based on *per capita* biomass of species), and thus indicates true structural differences that correct for variation in total biomass or density of predators or prey.

source of variation	community structure			
	biomass	density macrofauna	density zooplankton	body size
species	$F_{2,40} = 2.33^{**}$	$F_{2,40} = 4.41^{***}$	$F_{2,40} = 0.81$	$F_{2,40} = 2.00^*$
size	$F_{2,40} = 1.18$	$F_{2,40} = 0.94$	$F_{2,40} = 0.41$	$F_{2,40} = 0.49$
species $\times$ size	$F_{4,40} = 2.03^{***}$	$F_{4,40} = 2.15^{***}$	$F_{4,40} = 2.13^{**}$	$F_{4,40} = 1.96^{**}$

\* $p < 0.1$ , \*\* $p < 0.05$ , \*\*\* $p < 0.01$ .

was larger for *E. simplicicollis* than *P. longipennis*. Moreover, the direction in which centroids shifted also changed between size classes within species. For instance, the shifts from small to medium and medium to large *E. simplicicollis* were almost exactly opposite in direction (figure 2a). Consequently, differences among species increased or decreased with predator size, depending on the specific predator combination. Furthermore, small and large size classes could be more similar to each other than to medium size classes, even within a single predator species. Thus, size did not have a consistent directional (linear) effect on how predators affected the structure of the community, even within species. It was also a poor predictor for identifying similarities in the impact of predators on the community.

There was, however, some indication that the average dissimilarity among species scaled with size, but this pattern varied depending on how community structure was analysed (figure 3). Functional dissimilarity among species almost doubled as predator size increased from small to large when community structure was based on density of macro invertebrates or body size structure (size spectra), while differences decreased with increasing size for zooplankton community structure. This pattern was only significant for macro invertebrate density and body size spectra (both  $p < 0.05$ ) despite the large effect size (i.e. magnitude of change) for zooplankton. There was no clear pattern when community structure was based on biomass (figure 3), emphasizing the importance of characterizing communities in more than one way.

While we found a significant species effect for most metrics of community structure (table 1), differences among species did not stay constant with size. Consequently, differences between species were often smaller than differences within species. For example, when community structure was based on proportional biomass, communities with small *P. lydia*, medium *E. simplicicollis* and large *P. longipennis* were much more similar to each other than to any other size class treatment of conspecifics (figure 2a). Thus, just like size, species identity by itself was a poor predictor of functional similarity across all nine predator treatments.

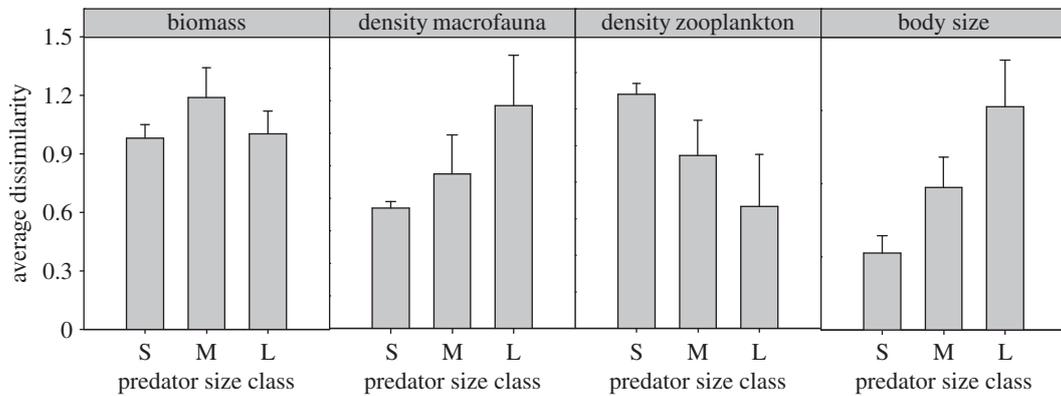
Interestingly, we found that the size spectra (i.e. proportional abundance of individuals within a given size class) of communities were also significantly affected by the interaction of size and species identity treatments (table 1), but the relative differences among treatments mostly did not reflect differences observed in community analysis based on biomass or density of species (figure 2d versus 2a–c). This indicates that the observed differences in species-based community structure were not simply driven by differences in size preference of predators.

## 4. Discussion

Given the apparent complexity of natural communities, it is not surprising that ecology has taken a reductionist approach to analyse food webs. The challenge is to identify the smallest common denominator that can adequately capture this complexity. In recent years, there has been an increasing debate about whether the traditional species-based approach should be replaced with a potentially more mechanistic, purely size-based approach to model natural communities [1,6,16,23]. However, each approach makes simplifying and largely untested assumptions about how variation across size classes or species influences species interactions and thereby the impact of consumers on communities (figure 1). Our results show that the basic assumptions of both approaches are violated in our system: differences in ecological interactions among size classes within species could rival or even exceed differences among species, and the effects of changing consumer size on the community structure were highly species specific. As a consequence, neither species nor body size alone was sufficient to explain functional differences among consumers. Instead, we found that effects of body size and species identity are not independent and that differences in interactions among consumers were driven by the synergistic effects of size and species identity. This indicates that we need to account for both body size and species identity of individuals to predict how changes in community structure influence the functioning of natural ecosystems.

### (a) Body size and the scaling of functional differences

Body size is increasingly recognized as a key trait influencing the dynamics and structure of natural communities [1,6,14,16,23,36–38]. This has led to the development of purely size-based approaches to characterize communities, which ignore species identity of organisms and group individuals simply by their size [1,7]. However, such purely size-based approaches assume (a) that interactions vary little among individuals within size classes across species, (b) that these differences within size classes do not change among size classes and (c) that functional similarity (i.e. impact on communities) should be highest for similar-sized organisms (figure 1b), although it is unclear how exactly functional differences scale with size. In our experiment, we found no evidence supporting assumptions (a–c). Instead, similar-sized individuals from different species could have vastly different effects on community structure, whereas consumers that differed up to eightfold in size could have almost identical effects,



**Figure 3.** Mean ( $\pm 1$  s.e.) dissimilarity among species as a function of size. Dissimilarities indicate how much the average community structure differs among species within a given size class (see Material and methods for details). To facilitate comparisons, dissimilarities were standardized (divided) by the total variation among all treatments for a given response variable. Note that differences were calculated based on all PCO axes derived from the full distance matrix and thus cannot be directly derived from the nMDS plots in figure 2 which only show two axes.

demonstrating that functional similarity was not higher within than between size classes. Importantly, we observed these differences in a group of closely related (all within the same family) generalist predator species with the same basic morphology, which should have increased the importance of size relative to species identity. This indicates that even among closely related organisms, the importance of species identity cannot be dismissed. Furthermore, we show that differences among consumer species within size classes did not remain constant across size classes, but increased or decreased depending on the specific consumer pair. Our results therefore challenge current purely size-based approaches to food web ecology and suggest that without accounting for species identity, we cannot predict the outcome of species interactions and impact of consumers on communities simply based on their body size.

Consistent with previous studies [2,3,13,24,39], our results demonstrate that differences in body size are still of key importance for determining functional differences among consumers. For instance, different size classes within species frequently differed dramatically in their impact on community structure. Theory suggests that such differences in ecological interactions among stages within species can also alter long-term dynamics of populations and communities [15,40,41]. However, we also found that these important effects of body size are highly species specific. Differences between species within size classes likely reflect differences in functionally important traits among consumers [24]. In our system, all three species are known to differ to some extent in several traits, including their microhabitat use (see the electronic supplementary material for details). Assuming that other species in the community differ as well in their microhabitat use, each consumer species would interact with a different compartment of the food web. Thus, even if similar-sized consumers would prefer similar-sized prey, they would consume different prey types, which would lead to differences in the proportional abundance of species (i.e. community structure). This is consistent with our findings that species differed in their impact on invertebrates in the vegetation; *E. simplicicollis* preferred vegetation and had the strongest impact on biomass of invertebrates in the vegetation (see the electronic supplementary material, figure S1), while *P. lydia*, which prefers leaf litter found in vegetation strongly reduced the abundance of taxa that also preferred leaf litter (e.g. *Caenis*; figure 2e,f). Recent studies indicate that differences in other traits, such as

feeding or hunting mode, or gape limitation, can also play an important role in altering how prey use changes with size [24,29,42]. Regardless of the exact mechanism, our results indicate that differences among species within a size class reflect species-specific trait differences which ‘constrained’ the functional similarity among similar-sized consumers. Such species-specific constraints of body size effects are likely to be common within a community, given that niche theory predicts that species with very similar traits are unlikely to occur in the same community [26,43,44]. Recent studies emphasize the need to include multiple ecological important traits of species to predict the complex structure of natural food webs [30,45]. Our results suggest that this approach should be expanded to include trait differences among stages within species.

A largely unresolved question is how functional differences among individual consumers should scale with size [2,3]. By using three species and multiple size classes within a single species in complex communities, we controlled for any species-specific effects that could confound this comparison. We found that functional differences do not necessarily scale positively with size, but can be nonlinear and increase or decrease depending on the specific species and response variable analysed. While this is consistent with one recent study on another dragonfly species [2], these results seem to contrast with other studies (including dragonflies) which found that differences in diets often increase with size differences among individuals [46,47]. In such scenarios, we could expect that differences in consumer impacts on communities increase with size. However, in complex communities, indirect interactions could result in functional differences among consumers that may not be proportional to differences in consumer diets [48,49]. In addition, many animal taxa are known to exhibit clear ontogenetic niche shifts in their diet (e.g. owing to habitat shift) [50,51], in which case differences among consumers may be completely unrelated to their relative size difference. Recent studies indicate that such ontogenetic niche shifts within species can scale up to alter community dynamics [15,40,41], whole ecosystem structure and processes [2,3], the stability of ecological networks and how communities respond to biodiversity loss [50]. Thus, it is unlikely that one universal rule determines the relationship between functional differences of consumers and their relative body size.

## (b) Reconciling size- and species-based approaches

While it may not seem surprising that both species identity and body size are important in determining the functional role of consumers, purely size- and species-based approaches have largely been used in parallel. Ecologists have only recently become aware that in reality both factors are likely to be important, and little was known about their relative importance or how they interact with each other [22]. Yet, to integrate size- and species-based approaches, we need to identify whether there are general relationships that link the effects of body size and species identity. Our study presents an important first step forward in this process by providing a conceptual framework and experimental test that explicitly quantifies how the effects of body size and species identity scale with each other. For instance, we found that differences among species can increase with size during ontogeny (depending on the response variable). If such general patterns hold across systems, this would provide an important link between the size spectra of communities and species diversity that could allow us to predict functional diversity within communities. On the other hand, our study also shows that the effect of size changes can vary considerably and seemingly unpredictably across species. Our study focused on three closely related species and it is unclear how patterns might change in different taxa or if species were not closely related. For instance, one might expect that species-specific effects increase if species are from different families or orders. However, one previous study demonstrates that even if species are from completely different taxa (beetle versus dragonfly larvae), functional differences among species still varied with size and rivaled or exceeded differences among species [3], suggesting that our findings are not system specific or restricted to close relatives. Unfortunately, unlike this study, the previous work did not examine species-specific differences

along a size gradient, so it could not detect whether functional differences increased or decreased. While these studies are an important first step towards resolving the role of body size and species identity on functional differences among organisms, future studies are needed that quantify functional differences among size classes for a large range of species to cover a large range of trait differences (e.g. feeding mode, habitat use, morphology, etc.) [30]. Only then can we identify whether there are some general patterns that can predict how species interactions change during ontogeny, how this is related to phylogenetic relationships of species and what the underlying mechanisms are.

The current and historical separation of size-based and species-specific approaches is largely one of convenience; grouping individuals only by species or solely by size is easier than keeping track of both. While either approach may give a close approximation to some natural systems, our results caution against blindly following one of these two exclusionary approaches because they simplify the inherent complexity of interactions structuring natural communities. Our results indicate that functional diversity is much more complex in natural communities than previously thought, and that losing species or size classes (e.g. owing to size-selective harvesting) will often have unanticipated consequences for natural ecosystems.

**Acknowledgements.** We thank A. Dunham for discussion and comments on earlier version of the manuscript, and A. Roman, E. Crowder, M. Braun, R. Nnaji and E. Sartain for assistance with sample analysis. We thank The National Forest Service and Sam Houston State University Center for Biological Field Studies for access to field sites.

**Data accessibility.** Community data with abundance matrix and biomass: DRYAD doi:10.5061/dryad.vp51n.

**Funding statement.** This work was supported by NSF DEB-0841686 to V.H.W.R.

## References

- Ings TC *et al.* 2009 Ecological networks: beyond food webs. *J. Anim. Ecol.* **78**, 253–269. (doi:10.1111/j.1365-2656.2008.01460.x)
- Rudolf VHW, Rasmussen NL. 2013 Ontogenetic functional diversity: size-structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**, 1046–1056. (doi:10.1890/12-0378.1)
- Rudolf VHW, Rasmussen NL. 2013 Population structure determines functional differences among species and ecosystem processes. *Nat. Commun.* **4**, 2318. (doi:10.1038/ncomms3318)
- Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ. 2006 Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313**, 966–968. (doi:10.1126/science.1128326)
- Harmon LJ, Matthews B, Des Roches S, Chase JM, Shurin JB, Schluter D. 2009 Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167–1170. (doi:10.1038/nature07974)
- Raffaelli D. 2007 Food webs, body size and the curse of the Latin binomial. In *From energetics to ecosystems: the dynamics and structure of ecological systems* (eds N Rooney, KS McCann, DLG Noakes), pp. 53–64. Dordrecht, The Netherlands: Springer.
- Marquet PA, Quinones RA, Abades S, Labra F, Tognelli M, Arim M, Rivadeneira M. 2005 Scaling and power-laws in ecological systems. *J. Exp. Biol.* **208**, 1749–1769. (doi:10.1242/jeb.01588)
- Jennings S, Mackinson S. 2003 Abundance–body mass relationships in size-structured food webs. *Ecol. Lett.* **6**, 971–974. (doi:10.1046/j.1461-0248.2003.00529.x)
- Cohen JE, Jonsson T, Carpenter SR. 2003 Ecological community description using the food web, species abundance, and body size. *Proc. Natl Acad. Sci. USA* **100**, 1781–1786. (doi:10.1073/pnas.232715699)
- Brose U *et al.* 2006 Consumer–resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417. (doi:10.1890/0012-9658(2006)87[2411:cbrinf]2.0.co;2)
- Riede JO, Brose U, Ebenman B, Jacob U, Thompson R, Townsend CR, Jonsson T. 2011 Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecol. Lett.* **14**, 169–178. (doi:10.1111/j.1461-0248.2010.01568.x)
- Reuman DC, Mulder C, Raffaelli D, Cohen JE. 2008 Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecol. Lett.* **11**, 1216–1228. (doi:10.1111/j.1461-0248.2008.01236.x)
- Woodward G, Blanchard J, Lauridsen RB, Edwards FK, Jones JI, Figueroa D, Warren PH, Petchey OL, Guy W. 2010 *Individual-based food webs: species identity, body size and sampling effects. Advances in ecological research*, pp. 211–266. New York, NY: Academic Press.
- Otto SB, Rall BC, Brose U. 2007 Allometric degree distributions facilitate food-web stability. *Nature* **450**, 1226–1229. (doi:10.1038/nature06359)
- Miller TEX, Rudolf VHW. 2011 Thinking inside the box: community-level consequences of stage-structured populations. *Trends Ecol. Evol.* **26**, 457–466. (doi:10.1016/j.tree.2011.05.005)
- Reiss J, Bridle JR, Montoya JM, Woodward G. 2009 Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* **24**, 505–514. (doi:10.1016/j.tree.2009.03.018)
- Mulder C, Elser JJ. 2009 Soil acidity, ecological stoichiometry and allometric scaling in grassland

- food webs. *Glob. Change Biol.* **15**, 2730–2738. (doi:10.1111/j.1365-2486.2009.01899.x)
18. Jennings S, Blanchard JL. 2004 Fish abundance with no fishing: predictions based on macroecological theory. *J. Anim. Ecol.* **73**, 632–642. (doi:10.1111/j.0021-8790.2004.00839.x)
  19. Jennings S, Melin F, Blanchard JL, Forster RM, Dulvy NK, Wilson RW. 2008 Global-scale predictions of community and ecosystem properties from simple ecological theory. *Proc. R. Soc. B* **275**, 1375–1383. (doi:10.1098/rspb.2008.0192)
  20. Woodworth-Jefcoats PA, Polovina JJ, Dunne JP, Blanchard JL. 2013 Ecosystem size structure response to 21st century climate projection: large fish abundance decreases in the central North Pacific and increases in the California Current. *Glob. Change Biol.* **19**, 724–733. (doi:10.1111/Gcb.12076)
  21. Petchey OL, Beckerman AP, Riede JO, Warren PH. 2008 Size, foraging, and food web structure. *Proc. Natl Acad. Sci. USA* **105**, 4191–4196. (doi:10.1073/pnas.0710672105)
  22. Woodward G, Andersen KH, Belgrano A, Blanchard J, Reiss J, Andrea B. 2011 *Body size and the (re)unification of ecology*. *Advances in ecological research*, pp. xv–xxix. New York, NY: Academic Press.
  23. Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH. 2005 Body size in ecological networks. *Trends Ecol. Evol.* **20**, 402–409. (doi:10.1016/j.tree.2005.04.005)
  24. Jacob U *et al.* 2011 The role of body size in complex food webs: a cold case. *Adv. Ecol. Res.* **45**, 181–223. (doi:10.1016/B978-0-12-386475-8.00005-8)
  25. Chalcraft DR, Resetarits WJ. 2003 Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology* **84**, 2407–2418. (doi:10.1890/02-0550)
  26. Resetarits WJ, Chalcraft DR. 2007 Functional diversity within a morphologically conservative genus of predators: implications for functional equivalence and redundancy in ecological communities. *Funct. Ecol.* **21**, 793–804. (doi:10.1111/j.1365-2435.2007.01282.x)
  27. Persson L, Greenberg LA. 1990 Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)–roach (*Rutilus rutilus*) interaction. *Ecology* **71**, 44–56. (doi:10.2307/1940246)
  28. Wirtz KW. 2012 Who is eating whom? Morphology and feeding type determine the size relation between planktonic predators and their ideal prey. *Mar. Ecol. Prog. Ser.* **445**, 1–12. (doi:10.3354/Meps09502)
  29. Klecka J, Boukal DS. 2013 Foraging and vulnerability traits modify predator–prey body mass allometry: freshwater macroinvertebrates as a case study. *J. Anim. Ecol.* **82**, 1031–1041. (doi:10.1111/1365-2656.12078)
  30. Boukal DS. In press. Trait- and size-based descriptions of trophic links in freshwater food webs: current status and perspectives. *J. Limnol.*
  31. Gilljam D *et al.* 2011 *Seeing double: size-based and taxonomic views of food web structure*. *Advances in ecological research*, pp. 67–133. New York, NY: Academic Press.
  32. McPeck MA. 1990 Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* **71**, 83–98. (doi:10.2307/1940249)
  33. Corbet PS. 1999 *Dragonflies: behavior and ecology of Odonata*, p. 829. Ithaca, NY: Cornell University Press.
  34. Anderson MJ. 2001 A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* **26**, 32–46.
  35. McArdle BH, Anderson MJ. 2001 Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**, 290–297. (doi:10.1890/0012-9658(2001)082[0290:FMMTCJ]2.0.CO;2)
  36. Brose U, Williams RJ, Martinez ND. 2006 Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* **9**, 1228–1236. (doi:10.1111/j.1461-0248.2006.00978.x)
  37. Yodzis P, Innes S. 1992 Body size and consumer–resource dynamics. *Am. Nat.* **139**, 1151–1175. (doi:10.1086/285380)
  38. De Roos AM, Persson L, McCauley E. 2003 The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecol. Lett.* **6**, 473–487. (doi:10.1046/j.1461-0248.2003.00458.x)
  39. Schneider FD, Scheu S, Brose U. 2012 Body mass constraints on feeding rates determine the consequences of predator loss. *Ecol. Lett.* **15**, 436–443. (doi:10.1111/j.1461-0248.2012.01750.x)
  40. Hin V, Schellekens T, Persson L, de Roos AM. 2011 Coexistence of predator and prey in intraguild predation systems with ontogenetic niche shifts. *Am. Nat.* **178**, 701–714. (doi:10.1086/662676)
  41. Persson L, de Roos AM. 2013 Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults. *Ecology* **94**, 1487–1498. (doi:10.1890/12-1883.1)
  42. Nakazawa T, Ohba S-y, Ushio M. 2013 Predator–prey body size relationships when predators can consume prey larger than themselves. *Biol. Lett.* **9**, 20121193. (doi:10.1098/rsbl.2012.1193)
  43. Chase JM, Leibold MA. 2003 *Ecological niches: linking classical and contemporary approaches*. Chicago, IL: University of Chicago Press.
  44. Loreau M. 2004 Does functional redundancy exist? *Oikos* **104**, 606–611. (doi:10.1111/j.0030-1299.2004.12685.x)
  45. Eklof A *et al.* 2013 The dimensionality of ecological networks. *Ecol. Lett.* **16**, 577–583. (doi:10.1111/Ele.12081)
  46. Woodward G, Hildrew AG. 2002 Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.* **71**, 1063–1074. (doi:10.1046/j.1365-2656.2002.00669.x)
  47. Munoz AA, Ojeda FP. 1998 Guild structure of carnivorous intertidal fishes of the Chilean coast: implications of ontogenetic dietary shifts. *Oecologia* **114**, 563–573. (doi:10.1007/s004420050481)
  48. Wootton JT. 1994 The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.* **25**, 443–466. (doi:10.1146/annurev.es.25.110194.002303)
  49. Schmitz OJ, Suttle KB. 2001 Effects of top predator species on direct and indirect interactions in a food web. *Ecology* **82**, 2072–2081. (doi:10.1890/0012-9658(2001)082[2072:Eotpsj]2.0.Co;2)
  50. Rudolf VHW, Lafferty KD. 2011 Stage structure alters how complexity affects stability of ecological networks. *Ecol. Lett.* **14**, 75–79. (doi:10.1111/j.1461-0248.2010.01558.x)
  51. Werner EE, Gilliam JF. 1984 The ontogenetic niche and species interactions in size structured populations. *Annu. Rev. Ecol. Syst.* **15**, 393–425. (doi:10.1146/annurev.es.15.110184.002141)