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

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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

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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

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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

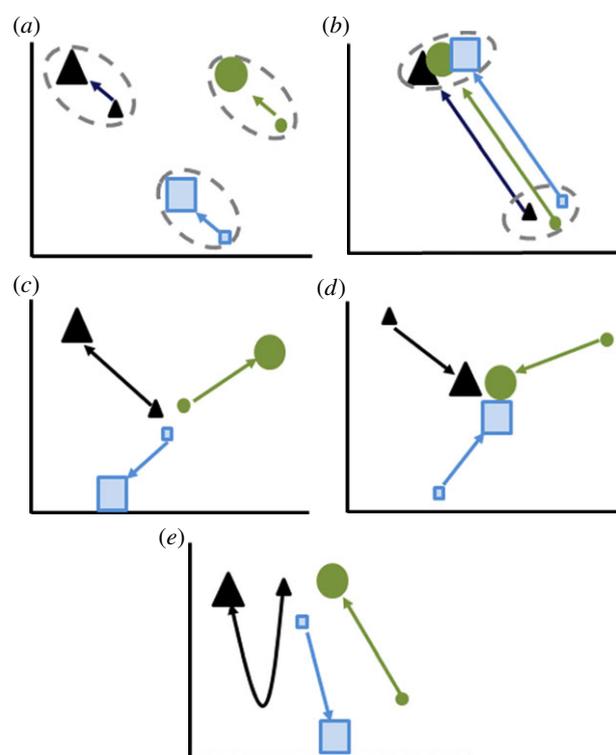


Figure 1. To determine how body size and species identity influence functional differences among consumers, we can use results from community ordination techniques (non-metric multidimensional scaling (nMDS) or PCO) summarizing the effect of individuals on a reference community. Symbols and colours represent 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 libellulid 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 3×3 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

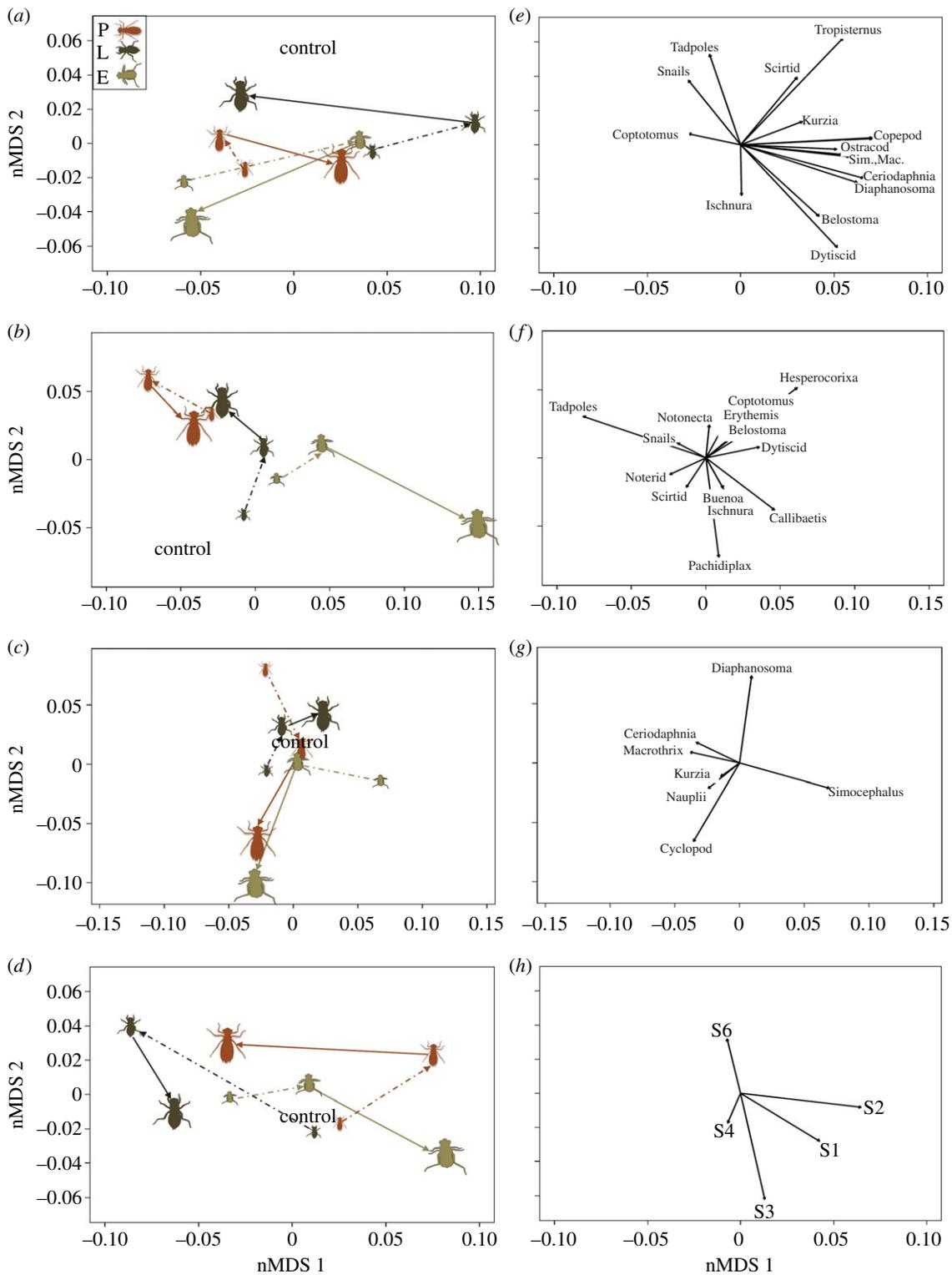


Figure 2. Consumer effect on community structure in the experiment. Two nMDS axes of proportional (a) biomass, (b) density of macrofauna, (c) density of zooplankton species and (d) proportional abundance of different animal size classes for different predator treatments. Symbols show the average community 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,

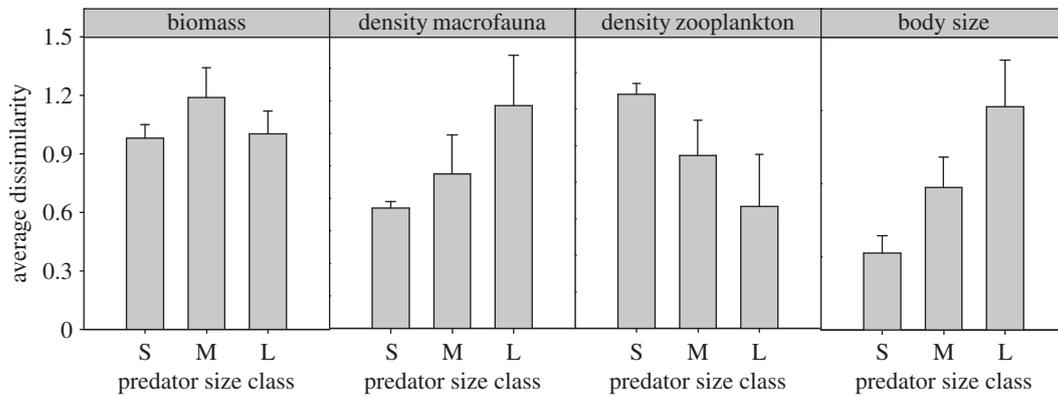


Figure 3. Mean (± 1 s.e.) dissimilarity among species as a function of size. Dissimilarities indicate how much the average community structure differs among species within a given size class (see Material and methods for details). To facilitate comparisons, dissimilarities were standardized (divided) 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.

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1 Online Supplement

2 **Table S1:** Per-capita size and mass and total biomass for different consumer treatments.

Focal dragonfly larvae	Average Head Width (mm)	Average Body Length (mm)	Average mass (mg)	Total predator biomass (mg)
<i>P. longipennis</i> -large	4.8	13.6	105.5	316.5
<i>P. longipennis</i> - medium	3.6	9.5	37.1	333.6
<i>P. longipennis</i> -small	2.6	7.35	14.4	344.8
<i>E. simplicicollis</i> -large	4.6	11.9	150.1	460.3
<i>E. simplicicollis</i> - medium	3.4	8.5	39.5	355.5
<i>E. simplicicollis</i> - small	2.1	5.8	12.7	347.4
<i>P. lydia</i> -large	3.2	13.2	102	306
<i>P. lydia</i> -medium	2.5	10.6	60	422
<i>P. lydia</i> -small	2.1	8.7	20	482.4

3

4

5 **Table S2:** Average abundance and dry mass of the most common taxa in the experiment.

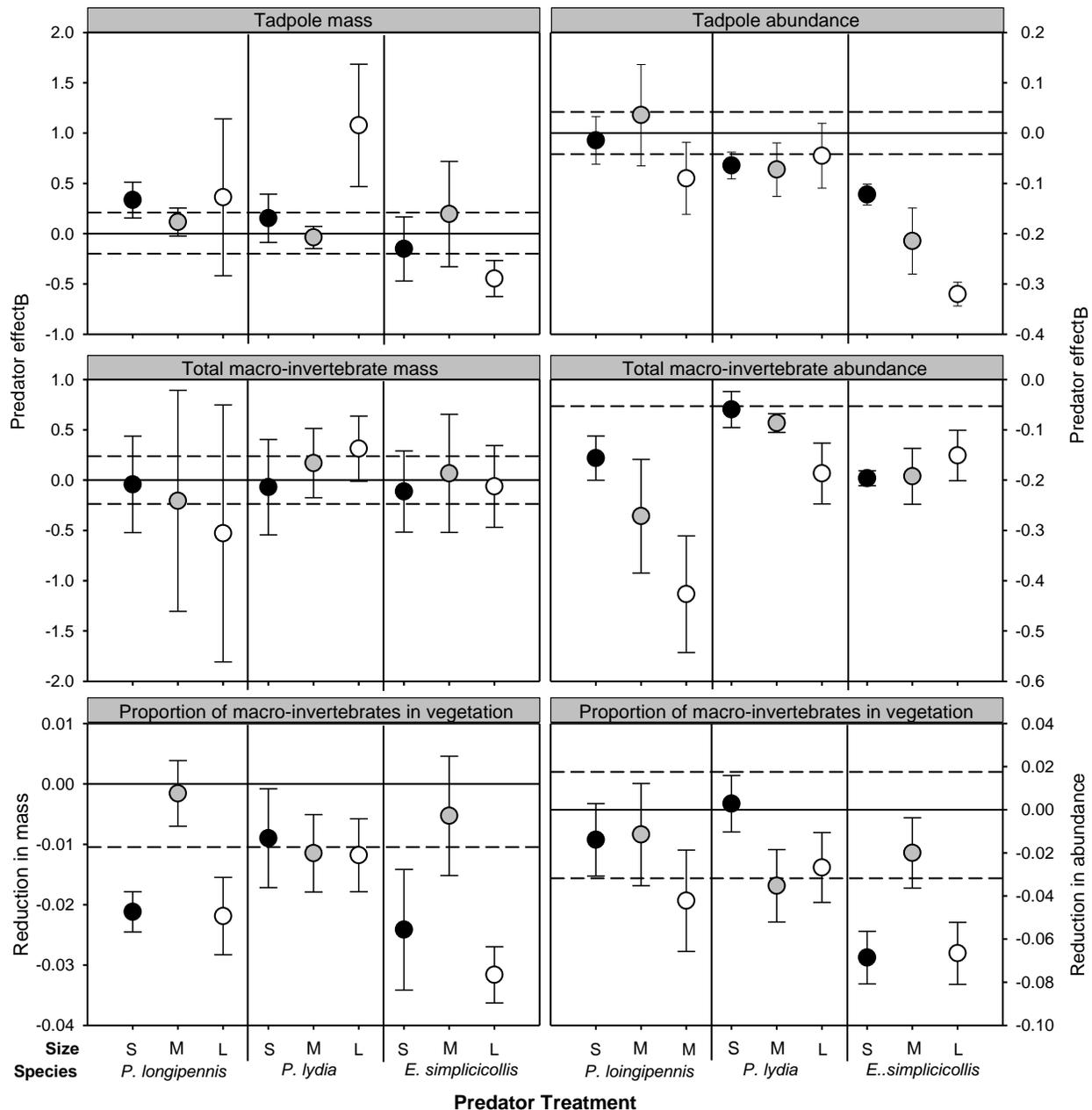
Species	Average abundance	Average dry mass (mg)
<i>Callibaetis sp.</i>	7.5	5.7
<i>Caenis sp.</i>	0.7	0.1
<i>Coptotomus loticus</i>	7.5	124.2
<i>Notonecta indica</i>	1.4	4.3
<i>Buena scimitar</i>	5.6	13.7
<i>Dytiscid</i>	0.6	1.6
<i>Noterid</i>	0.6	1.7
<i>Belostoma sp.</i>	1.2	4.8
<i>Hesperocorixa nitida</i>	20.4	349.5
<i>Tropisternus sp.</i>	1.3	25.7
<i>Ischnura sp.</i>	1.9	2.5
<i>Physid snail</i>	1.05	2.7
<i>Erythemis simplicicollis</i>	1.45	1.1
<i>Pachydiplax longipennis</i>	6.55	5.0
<i>Rana clamitans</i>	31.4	88.0
<i>Cyclopoid</i>	209.1	3.1
<i>Cyclopoid nauplii</i>	7.7	10.7
<i>Diaphanosoma sp.</i>	164.1	3.0
<i>Ceriodaphnia sp.</i>	37.4	0.2
<i>Simocephalus sp.</i>	68.9	6.8
<i>Kurzia sp.</i>	4.75	0.1
<i>Macrothrix sp.</i>	19.3	1.2
<i>Ostracod sp.</i>	8.0	0.02

Table S3: Effects of consumer size and species identity on abundance and mass of trophic groups. Treatment effects indicate the standardized per-unit biomass effects of predators on ecosystem traits relative to the control and corrected for potential differences in predator biomass. Degrees of freedom were adjusted when block effects were included in the analysis and when variances were unequal among treatments (tadpole abundance and mass). P values are based on general linear models.

Source of variation	<u>Tadpole</u>		<u>Macro invertebrates</u>			
	Abundance	Mass	Total		% in vegetation	
			Abundance	Mass	Abundance	Mass
Species	$F_{2,19.2} = 12.04^{****}$	$F_{2,13} = 1.54$	$F_{2,40} = 6.58^{**}$	$F_{2,45} = 2.34$	$F_{2,40} = 4.59^*$	$F_{2,40} = 1.43$
Size	$F_{2,19.3} = 2.38$	$F_{2,15.4} = 0.20$	$F_{2,40} = 3.01^\dagger$	$F_{2,45} = 0.18$	$F_{2,40} = 2.50^\dagger$	$F_{2,40} = 4.16^*$
Species*Size	$F_{4,15.3} = 2.14$	$F_{4,13.8} = 1.02$	$F_{4,40} = 1.86$	$F_{4,45} = 0.97$	$F_{4,40} = 2.44$	$F_{4,40} = 1.22$

$^\dagger P < 0.1$, $^\ddagger P < 0.06$, $* P < 0.05$, $** P < 0.01$, $*** P < 0.001$, $**** P < 0.0001$

1 **Figure S1:** Mean (± 1 SE) treatment effects on abundance and (dry) biomass of tadpoles and total
 2 macro-invertebrates (all invertebrates excluding zooplankton), and reduction in the proportion of
 3 macro-invertebrates found in vegetation. Predator effect_B indicates the standardized per unit-
 4 biomass effect (see Methods for details) of predators within a given treatment on the respective
 5 ecosystem trait relative to the predator free control. Effects on macro-invertebrates in vegetation
 6 indicate how much the proportional abundance or mass of invertebrates was reduced in a given
 7 treatment. Because this comparison was already based on proportions, it was not corrected for
 8 predator biomass. Dashed lines indicate 95% confidence intervals for control. In general
 9 treatments differed significantly from the control if error bars were outside the confidence
 10 interval.



12 **Methods**

13 *Focal Species* – To determine how the ecological interactions of individuals are influenced by
14 their size and species identity we focused on a guild of larvae of three libellid dragonfly
15 species: *Erythemis simplicicollis*, *Plathemis lydia*, and *Pachydiplax longipennis*. We focused on
16 dragonfly larvae because they are known to be generalist predators that can strongly influence
17 the structure of fishless pond communities, and because dragonfly populations are highly size
18 structured. The three specific species were chosen because they are among the most abundant
19 species in our study area and commonly co-occur in fishless pond communities in South East
20 Texas. While dragonfly larvae are generalists and thus have the potential to strongly overlap in
21 their diet, all three species differ to some extent in their morphology, which in part reflects
22 differences in micro-habitat use. *E. simplicicollis* can be found in the leaf litter but prefers to
23 perch in the vegetation. *P. longipennis* is most commonly found in leaf litter but can sometimes
24 be found in vegetation, while *P. lydia* is never found in the vegetation and prefers to burrow into
25 the sediment or move through the leaf litter. These differences in micro-habitat use observed in
26 the field were recovered in the experiment, where *E. simplicicollis* was the only species found in
27 the vegetation, and the *P. lydia* treatment was the only treatment with clear signs of “burrowing
28 trails” in the sediment.

29 *Experimental design* – The experiment used a 3 x 3 factorial design which independently
30 manipulated the species identity (3 species) and size (small (S), medium (M), large (L)) of
31 individuals plus a control without a focal predator addition, resulting in a total of 10 treatments.
32 Each treatment was replicated six times and arranged in a completely randomized block design.
33 We picked the three size classes to keep the size and mass of individuals within a size class as
34 constant as possible across species within the constraints imposed by the natural differences in

35 body morphology. None of the large size classes was in the final instar as larvae typically stop
36 feeding a few days before metamorphosis. Large instars were on average ~3 and ~8 times
37 heavier than medium and small instars across species, respectively (Table 1). Thus, to keep
38 average biomass comparable across size treatments, we used the same ratios (L:M:S = 1:3:8) to
39 adjust the number of individuals per mesocosm, resulting in a final density of: L = 3, M = 9, S =
40 24 individuals per mesocosm. This assured that total dragonfly biomass varied on average less
41 than 6% (range 2.5%-7.8%) across size treatments while keeping total density constant within a
42 size treatment across species (Table 1). We found no significant difference in the proportional
43 survival among predator treatments (GLM with binomial error, $\chi^2 = 0.509$, $P > 0.999$). While
44 densities are at the higher end for small stages, all densities are within the range observed in
45 nature.

46 *Experimental communities* – Experiments were carried out in mesocosms consisting of a 62.5 L
47 plastic container (L x W x H: 67 cm x 41 cm x 31cm) filled to a depth of 25 cm with
48 reconditioned tap water and a ~2cm deep sand layer at the bottom. All mesocosms were set up in
49 six spatial blocks in an open field at the South Campus Research facility of Rice University,
50 Houston, TX. All mesocosms were covered with white plastic lids, and 60% shade cloth covered
51 the full experimental array. To account for potential differences in micro-habitat use among
52 species, we created three equally sized habitat zones within a mesocosm arranged in parallel
53 band: the first zone consisted of only leaf litter and sand without emerged vegetation, the second
54 zone contained leaf litter, sand, and emerged vegetation, and the last zone consisted of plants and
55 sand without leaf litter. This gradient mimicked the natural transition in a habitat structure from
56 the margins to the center of a pond. Leaf litter consisted of 15 g (dry mass) leaf mixture (mostly
57 oak and pine leaves collected from the margin of a local fishless pond) evenly spread across one

58 half of the mesocosm above the sand. To standardize plant cover, we evenly spaced four plastic
59 aquarium plants (*Ambulia sp.*) which covered ~70% of the water column of the plant section. In
60 addition, we added 22.5 g (wet mass) of floating natural vegetation (*Utricularia sp.*) obtained
61 from a local fishless pond. To create a complex natural animal community each tank received
62 1,300 mL of sifted (mesh size 120 μm) and concentrated benthos and 250 mL of concentrated
63 zooplankton and phytoplankton collected from two local invertebrate ponds. Samples were taken
64 haphazardly from all micro-habitat types. In addition, each tank received 25 *Hesperocorixa*
65 *nitida*, 8 adult *Coptotomus* beetles, 4 adult *Buena scimitra*, 4 *Belostoma sp.* nymphs, and 50
66 recently hatched *Rana clamitans* tadpoles. This setup assured a diverse range of vertebrate and
67 invertebrate prey consisting of 47 species. This assembly protocol likely introduced some degree
68 of random variation in community structure (for zooplankton and small invertebrates) across
69 ponds. However, similar variation occurs across natural communities, and it only means that our
70 results are conservative and require a large effect size of a given treatment to be significant.

71 Two days later, we initiated the experiment by adding dragonfly predators on August 23rd 2013,
72 and the experiment was terminated on August 30th 2013. Because dragonflies can grow quickly
73 this relatively short period was necessary to preserve size differences among treatments. At the
74 end of the experiment, tanks were sampled destructively in three steps. First, we used an
75 aquarium net to remove all the floating vegetation and preserved all the embedded invertebrates
76 separately (“vegetation” community sample). Then, we collected all macro-invertebrates (body
77 size > ~1 cm) remaining in the tanks using the same net, and sifted through the sand. Finally, we
78 filtered the entire aquatic habitat through an 80 μm mesh and preserved the content. All
79 vertebrates and invertebrates were stored in 75% ethanol solution and stored at -25°C until
80 further analysis. All amphibians were first euthanized in MS-222 prior to preservation. All

81 procedures were in compliance with ethical guidelines for animal use and approved by the
82 Institutional Animal Care and Use Committee (IACUC Protocol #A09022601).

83 *Response variable* – We quantified animal biomass and community structure by counting,
84 measuring, and weighing > 36,560 individuals from 47 species covering a diverse range of taxa,
85 functional groups and size classes (Table S2). We calculated total macro-invertebrate (all
86 invertebrates excluding zooplankton) biomass by combining all samples from a mesocosm and
87 drying the sample at 60°C for 48h. Species specific dry masses were calculated by measuring
88 body length or head width of individuals using photographs and image analysis (Image J) and
89 converting these measurements into dry mass using our own and published (1) length-mass
90 relationships. The average size of species did not vary significantly among treatments. Thus, we
91 used the average (across treatments) body size of a given species to estimate species specific dry
92 mass. The obtained estimates closely followed the pattern of the actual dry mass without
93 treatment bias, although it consistently overestimated the total dry mass. Zooplankton
94 community was determined by identifying and counting all individuals within a random
95 subsample (1/5 of the entire zooplankton sample).

96 Community structure can change in at least two non-exclusive ways: changes in absolute
97 abundances and changes in relative abundances. Thus, we calculated community structure based
98 on 1) total and 2) proportional abundance or biomass of each species (i.e. proportion of a species
99 relative to the total community biomass or abundance of an experimental pond). We were
100 primarily interested in whether dragonfly predators differed in their direct and indirect
101 interactions (i.e. whether the relative strength of interactions changed with species and/or size)
102 rather than in their total consumption rates (which was analyzed separately). Thus, we focused
103 on proportional abundances in the main text, but the patterns were largely similar for analyses

104 based on absolute abundances. Biomass specific analysis included all vertebrate and invertebrate
105 species, with zooplankton biomass scaled up to whole mesocosm volume. Because of their high
106 densities, zooplankton species would have strongly dominated the density based community
107 analysis (~80% of differences among treatments even after fourth root transformation). Thus, we
108 analyzed density based community structure separately for zooplankton and macro-fauna (all
109 other invertebrates + vertebrates). Overall, including or excluding zooplankton did not alter the
110 main results. Finally we analyzed changes in the size-structure (spectrum) of the community by
111 comparing abundances of individuals within \log_{10} size classes based on the average per-capita
112 dry mass of species. Choosing different size bins did not change the results, indicating that the
113 analysis was robust to changes in bin size. In cases where differences in biomass or abundance
114 were large among species (or size classes) we used square root or fourth root transformation of
115 the data (see Table 2) (2). Transformation did not alter our significant results, but avoided that
116 results were driven by a few abundant or heavy species. For the final analyses we removed
117 species that were present in less than 5% of the mesocosms (2). Including them did not alter the
118 results.

119 *Statistical analysis* – Because each of the nine predator “groups” were allowed to interact with
120 the same reference community, differences in the final community structure reflect all the
121 differences in the direct and indirect interactions of the focal predators with the prey community
122 among the predator groups, i.e. their functional differences. Thus, using a combination of
123 multivariate non-parametric permutational statistics, we can compare the community structure of
124 each treatment to answer several hypotheses about the relative and joint effects of size vs.
125 taxonomy for determining differences among predators (Fig. 1 A-E). First, we tested for overall
126 differences in community structure among treatments using PERMANOVA (3, 4), with size and

127 species as fixed factors and spatial block as random factor. If there is no significant interaction,
128 size and taxonomy have independent effects, and we can partition the variance explained by each
129 factor to determine their relative importance (i.e. distinguish between Fig.1A and B). However, a
130 significant interaction among size and species identity treatments would indicate that size and
131 taxonomic effects are not independent, i.e. functional similarity among species changes with size
132 (Fig. 1C-E). Given a significant interaction effect, we can then determine whether functional
133 similarity predictably scales with size, (e.g. whether it increases or decreased with size) (Fig. 1C,
134 D), using two approaches to compare distances among treatment centroids. First, we can use
135 PERMDISP (5) with size as fixed factor to calculate the average distances of replicates within a
136 treatments to the centroid of the respective treatment; the larger the distance, the more dissimilar
137 treatments are. Given equal variances among treatments, a significant effect would then indicate
138 an overall directional change in functional similarity of species with size (Fig. 1C,or D).
139 However, the drawback of this approach is that it does not separate within vs. between species
140 variation. To overcome this limitation, we calculated the average distance among treatments
141 following Huygens' theorem as $\sqrt{(\text{sum of all squared inter-centroid distances of all species}$
142 $\text{treatments within a given size class / divided by the number of species})}$. Comparing these
143 distances among size treatments indicates whether and how differences among species change
144 with size. Both approaches showed the same pattern, so for simplicity we only present the results
145 of this analysis in the main text. If there are no clear differences, this suggests that there is no
146 general trend for how functional similarity changes with size but instead patterns are driven by a
147 complex interaction of taxonomic and size effects (e.g. Fig. 1E) which can be revealed by visual
148 inspection of nMDS plots.

149 All community structure analyzes were performed based on Bray-Curtis similarity metrics using
150 the software PRIMER 6 & PERMANOVA+. Permutation analyses were carried out using 999
151 permutations and were based on centroids. Centroid distances among species within size classes
152 were calculated as the distance between principle coordinates (PCO) centroids using PRIMER 6
153 & PERMANOVA+. We visualized community structure with nonmetric multidimensional
154 scaling plots (nMDS) using the R statistical computing environment with the packages “Ecodist”
155 to calculate dissimilarity metrics, and “Vegan” to draw nMDS plots and create species vectors.

156 To gain additional insights about functional differences among predators, we also examined the
157 per- biomass effect of predators on the abundance and biomass of tadpoles and macro-
158 invertebrates, and the proportion of macro-invertebrates in the vegetation (to examine micro-
159 habitat specific effects) using separate generalized linear mixed models (GLMM) with block as a
160 random factor and species and size as fixed factors in SAS® 9.3 (Littell et al. 2006). If block was
161 not significant it was dropped from the analysis. To account for potential differences in total
162 biomass across treatments, we calculated the biomass corrected effect ($effect_B$) of predators for a
163 given ecosystem response variable (X) as $X_B = (X_{JP} - X_C) / B_J$, where X_{JP} indicates the value of a
164 given response variable for mesocosm P in predator treatment J, X_C indicates the average of the
165 respective response variable in the control, and B_J is the average final total dry mass of predators
166 in treatment J. Positive values of X_B indicate that the respective treatments had larger values than
167 the control and negative values the opposite. Except for tadpole biomass, error distribution of
168 response variables was best described by a normal distribution and Bartlett tests indicated no
169 significant heteroscedasticity across treatments. For tadpole biomass we accounted for the
170 significant heterogeneity in variance among treatments by using a likelihood estimation of the

171 variances in the “proc mixed” procedure in SAS and corrected the degrees of freedom using the
 172 Kenward-Roger correction (6). Results are shown in Table S3 and Figure S1.

173

174 **Results**

175 *Per-biomass effect of predators*

176 The biomass-specific effect of predators differed significantly among species for some response
 177 variables (see Table S3), but the effect of size often increased with per-capita mass of predators
 178 (Fig. S1). For instance, tadpole abundance was only significantly reduced (relative to the control)
 179 by *E. simplicicollis*, and this effect was stronger for large than for small *E. simplicicollis* (Fig.
 180 S1). All but small *P. lydia* significantly reduced total macroinvertebrate abundance relative to the
 181 control, but only for *P. longipennis* and *P. lydia* did this effect increase with predator size (Fig.
 182 S1). The proportion of macroinvertebrates (both mass and abundance) in the vegetation was
 183 significantly influenced by size treatments. This effect was largely driven by the fact that *P. lydia*
 184 larvae had no significant effect relative to the control regardless of size, while small and large
 185 size classes differed for *P. longipennis* (only for abundance) and *E. simplicicollis* (Fig. S1).

186

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 189 macroinvertebrates in North America with particular reference to the southeastern United
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