

Ontogenetic diversity buffers communities against consequences of species loss

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Abstract

1. Biodiversity can be measured at multiple organizational scales. While traditional studies have focused at taxonomic diversity, recent studies have emphasized the ecological importance of diversity within populations. However, it is unclear how these different scales of diversity interact to determine the consequence of species loss.
2. Here we asked how predator diversity and presence of ontogenetic diversity within predator populations influences community structure. Ontogenetic diversity arises from shifts in the traits and ecology of individuals during ontogeny and it is one of the biggest sources of intraspecific diversity. However, whether it dampens or strengthens the negative consequences of with species loss is poorly understood.
3. To study the interaction of species diversity and ontogenetic diversity, we experimentally manipulated predator species diversity and diversity of developmental stages within focal predator species and analysed their joint effect on predator and prey survival, biomass and prey community structure in experimental pond systems.
4. While individual effects of ontogenetic diversity were often species specific, losing predator species from the community often had a much smaller or no effect on prey survival, biomass or community structure when all predator populations had high ontogenetic diversity. Thus, ontogenetic diversity within populations buffered against some of the consequences of biodiversity loss at higher organizational levels. Because the experiment controlled mean per capita size and biomass across structured versus unstructured populations, this pattern was not driven by differences in biomass of predators. Instead, results suggest that effects were driven by changes in the functional roles and indirect interactions across and within species. This indicates that even if all environmental conditions are similar, differences in the intrinsic structure of populations can modify the consequences of biodiversity loss.
5. Together, these results revealed the importance of ontogenetic diversity within species for strengthening the resilience of natural communities to consequences of biodiversity loss and emphasize the need to integrate biodiversity patterns across organizational scales.

KEYWORDS

biodiversity and ecosystem functioning, intraspecific variation, ontogeny, size structure

1 | INTRODUCTION

Biodiversity is linked to the functioning of natural ecosystems (Cardinale et al., 2012; Hillebrand & Matthiessen, 2009; Lefcheck et al., 2015; Tilman et al., 2014). For instance, changes in predator species diversity can threaten a variety of ecosystem attributes, such as control of prey and plant abundance, community structure and diversity (Bruno & O'Connor, 2005; Douglass et al., 2008; Finke & Snyder, 2010). However, it is much less clear at what level of biological organization we need to resolve diversity to accurately predict how communities respond to biodiversity loss. Classical approaches have largely focused on biodiversity at the species level or higher (e.g. functional guilds), but this approach has been criticized because it ignores the substantial variation that exists within species (Bolnick et al., 2011; Harmon et al., 2009; Nakazawa, 2015; Oliver et al., 2015; Raffaelli, 2007; Raffard et al., 2019; Rudolf & Lafferty, 2011; Violle et al., 2012). Biodiversity measured at the species level may be poorly correlated with the actual erosion of functional diversity, which could partially explain why effects of species loss can vary substantially across studies (van der Plas, 2019).

The greatest source of intraspecific variation stems from differences in ontogenetic stage (De Roos & Persson, 2013; Nakazawa, 2015; Rudolf, 2020; Zhao et al., 2014). Fundamental traits such as size, behaviour, resource use and defence against consumers vary considerably between ontogenetic stages (Werner & Gilliam, 1984; Yang & Rudolf, 2010). Ontogenetic stages can differ substantially in their ecological niche and their impact on the dynamics and structure of populations, communities and ecosystem processes (De Roos & Persson, 2013; Griffin & Silliman, 2018; Miller & Rudolf, 2011; Reum et al., 2019; Rudolf & Rasmussen, 2013a; Rudolf et al., 2014; Start, 2018; Toscano & Griffen, 2012). Functional differences between stages within species can rival or even exceed differences across species (Rudolf & Rasmussen, 2013b; Rudolf et al., 2014). While these studies confirmed that functional differences among ontogenetic stages are ubiquitous and important in nature, the focus has been on ontogenetic diversity within a single species in a given community context, but not how ontogenetic diversity interacts with variation in community structure and species diversity. It remains unknown how ontogenetic functional diversity interacts with taxonomic diversity to influence the structure and functioning of ecosystems.

The consequences of species loss for ecosystems depend on at least three factors: the identity of lost species, how this loss alters functional diversity and whether indirect interactions between species exist that can alter their individual impacts on the ecosystem (Cardinale et al., 2012; Duffy et al., 2007). Ontogenetic niche shifts have the potential to alter all three factors and therefore could also change how the loss of biodiversity affects ecosystems. Ontogenetic stages within populations can differ substantially

in their functional roles. Changes in the stage diversity of populations can therefore also alter the 'functional identity' of species and hence change functional diversity within communities (Griffin & Silliman, 2018; Rudolf & Rasmussen, 2013a, 2013b; Toscano & Griffen, 2012). Furthermore, changing the stage structure of populations typically also changes food web structure (i.e. complexity, vertical structure and interaction strengths) and what direct and indirect interactions are possible. When predator populations consist of small and large stages, this allows large stages to consume small stages, resulting in cannibalism and intra-guild predation (Magalhaes et al., 2005; Polis & Holt, 1992; Rudolf, 2012). This, in turn, alters food web complexity (e.g. increases number of trophic levels, connectance and predation 'loops'; Woodward et al., 2010) and the potential for consumptive and non-consumptive indirect interactions (Carter et al., 2018; Krenek & Rudolf, 2014; Rudolf, 2008a, 2008b, 2012; Rudolf & Armstrong, 2008; Toscano & Griffen, 2012). Trophic complexity and indirect interactions among species determine how losing biodiversity affects ecosystems (Casula et al., 2006; Duffy et al., 2005, 2007; Finke & Denno, 2005; Ives et al., 2005; Wang & Brose, 2018). Together, this suggests that losing a species from a community could have very different consequences depending on the diversity of stages present within species. Testing this hypothesis is particularly important given that stage-structures of populations vary substantially between species, seasons or years and communities (Rudolf, 2012; Urban, 2007; Wissinger, 1989, 1992).

Here we used an experimental approach to determine how biodiversity loss at the taxonomic level interacts with ontogenetic diversity within species. Specifically, we independently manipulated the diversity of developmental stages and species diversity within a guild of predators in experimental pond communities to examine how ontogenetic diversity within species influences (a) the impact of predator species on prey community (functional role), and (b) the consequences of biodiversity loss (at the species level) for the prey community. Overall, results indicate that the ontogenetic diversity within species not only determined the functional role of predators but also buffered the communities from consequences of biodiversity loss at the species level.

2 | MATERIALS AND METHODS

2.1 | Study system

We focused on aquatic stages of three predators: the dragonfly *Anax junius*, the giant water bug *Belostoma lutarium* and larvae of the diving beetle *Cybister fimbriolatus*. These species commonly co-occur in fishless pond communities in North America (Gunzburger & Travis, 2004). They are all important apex predators in their final aquatic stage, but they represent different taxonomic orders and

consequently vary substantially in their functional traits, including morphology, behaviour and ecology (Gunzburger & Travis, 2004; Klecka & Boukal, 2013; Rudolf & Rasmussen, 2013a). *Anax junius* has chewing mouth parts, internal gills, and generally hunts by resting on or walking across the substrate surface to ambush its prey (Rudolf & Armstrong, 2008). In contrast, *B. lutarium* and *C. fimbriolatus* both have sucking mouth parts, and need to come to the surface to breathe with posterior respiratory appendages and spend time in the substrate but also swimming in the open water column and rest near the surface (Culler et al., 2014; Yee, 2010). All three predators are generalists and feed on a variety of prey species, including tadpoles. *Anax junius* tends to be most efficient tadpole predator, followed by *C. fimbriolatus* and then *B. lutarium* (Gunzburger & Travis, 2004; Relyea, 2001), but all three predators are known to elicit anti-predator behaviour and morphological changes in tadpoles (Relyea, 2003). Stable isotope suggest that *B. lutarium* seems to have a wider diet range than *C. fimbriolatus* (Rudolf, 2020), but none of the three species are likely to consume zooplankton given the size ranges used in this experiment (Klecka & Boukal, 2012). Furthermore, experiments and field observations indicate that each species exhibit clear ontogenetic niche shifts, that is, the interactions and resource use of individuals change during development (Rudolf, 2020; Rudolf & Rasmussen, 2013b). Smaller stages in each species generally prefer smaller prey and tend to use different microhabitats than larger conspecifics. As a consequence, stages differ considerably in their functional role, that is, their effects on

prey community structure, primary producers and ecosystem productivity (Rudolf & Rasmussen, 2013a, 2013b). Finally, cannibalism and intra-guild predation are common in all three species, with larger stages consuming smaller stages (Carter et al., 2018; Culler et al., 2014; Rudolf & Rasmussen, 2013b).

2.2 | Experimental design

We examined the interaction of diversity within and between species by jointly manipulating species identity and diversity, and the stage diversity within populations (Figure 1). First, we created two stage diversity treatments for populations of given species: 'unstructured', where all individuals were in similar developmental stages, and 'diverse', where individuals within a population represented a diverse range of developmental stages. This stage diversity treatment was crossed with four predator treatments: three single predator treatments with only either *Anax*, (A), *Belostoma* (B) or *Cybister* (C), and a high diversity treatment with all three predators (ABC). Together with a predator-free control treatment, this resulted in a total of nine predator treatments (control + 2 stage treatments × 4 species treatments), each replicated five times ($N = 45$).

We used an additive design to manipulate taxonomic diversity that held density constant (eight individuals/mesocosm) for each species in the high diversity treatment, which means that total predator densities (across all three species) was higher in high diversity

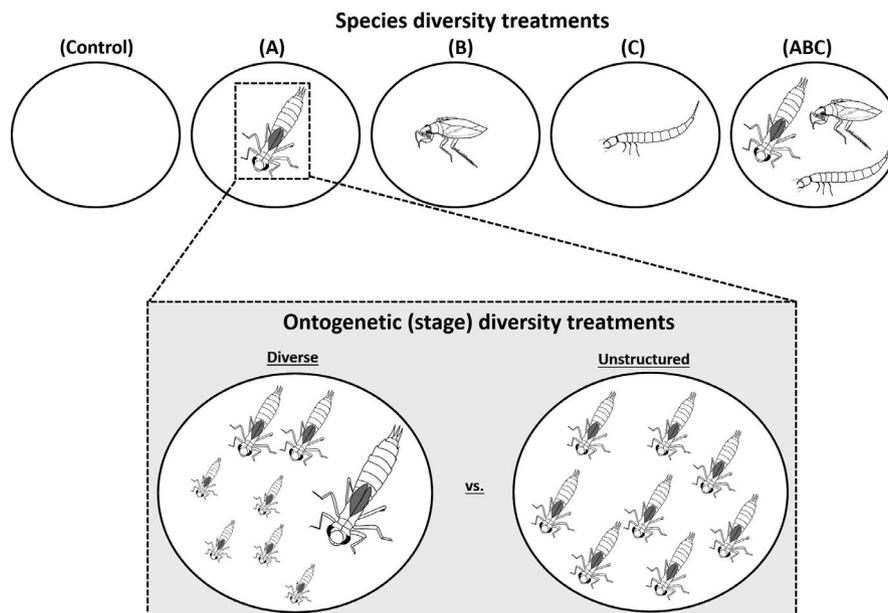


FIGURE 1 Experimental design to study how species diversity and ontogenetic diversity interact to drive the effects of species loss. One predator-free control and four predator treatments were used to manipulate predator diversity, including three single predator treatments with either only dragonfly *Anax junius* (A), giant water bug *Belostoma lutarium* (B) or diving beetle *Cybister fimbriolatus* (C) and a high diversity treatment with all three predators (ABC). The four predator diversity treatments were then cross with two ontogenetic (stage) diversity treatments where each predator population was either 'unstructured', with all individuals from a similar developmental stage, or 'diverse', with a wide range of developmental stages. Together with a predator-free control treatment, this resulted in a total of nine predator treatments (control + 2 stage treatments × 4 species treatments), each replicated five times ($N = 45$). We used an additive design to manipulate species diversity that held density (eight individuals/mesocosm) and biomass of each species constant across predator and ontogenetic diversity treatments

(ABC) treatment. This design was necessary to (a) allow us to manipulate stage diversity within species while maintaining natural densities and equal biomass for each species, and (b) avoid confounding changes in intraspecific density with species diversity effects.

The focal predators naturally differ in the number of developmental stages, and these differences were reflected in the stage diversity treatment; *Anax* had the highest diversity of stages (seven stages) followed by *Belostoma* (four stages) while *Cybister* naturally has the lowest diversity (three stages). The identity and total number of individuals within each stage was designed so that it reflected natural relative abundance of stages while keeping total density constant and mean per capita (and thus total) biomass similar across focal species and stage diversity treatments (Table S1). This substitutive design ensured that any differences among predators or stage diversity treatments are not driven by differences in initial density or biomass.

2.3 | Mesocosm setup

Experiments were carried out in mesocosms that were designed to capture basic environmental conditions and communities of the natural ponds used by the focal species. Each mesocosm consisted of a 300-L cylindrical PVC containers covered with a 60% shade cloth lid to prevent unwanted colonization by large invertebrates or amphibians, and to contain metamorphs and emerging insects. Mesocosms were spaced by ~60 cm in a 5 × 9 grid in an open field at the South Campus Research Facility of Rice University in Houston, TX. We used a complete randomized spatial block design to assign treatments, with each spatial block representing one row (nine mesocosms).

Mesocosms were first filled with dechlorinated tap water on 12 July 2016. Three days later we added 400 ml concentrated zooplankton and phytoplankton to each replicate. On the following day we added nutrients (0.265 g sodium phosphate + 6.427 g sodium nitrate) to each mesocosm and 1,660 ml dried leaf litter (mix of pine and oak leaves) raked from the margins of fishless ponds. To simulate structural habitat complexity of different vegetation types and provide a potential refuge of small prey and predators, we added two large bunches of nylon (deer) netting on July 26, one at the bottom of the tank and one floating beneath the water surface. Finally, we added 1,250 ml of concentrated benthic animal mixture on July 27, and 60 *Rana* (*Lithobates*) *clamitans* and 300 *Bufo* (*Incilius*) *valliceps* tadpoles on July 29. Benthic animal samples were collected by sifting sediment and leaf litter from fishless ponds. *Bufo* and *Rana* tadpoles were 2- to 3-day-old hatchlings and represented a random mix from several clutches per species incubated in the laboratory. All organisms and leaf litter were collected from fishless ponds where all three predator species naturally occur, located in Huntsville and Davy Crockett National Forrest, TX. The experiment was initiated with predator addition on July 30 and ended on August 11. This period was based on previous studies (Rudolf & Rasmussen, 2013b) and aimed to maximize detection of predator effects while maintaining

differences between stages and minimizing the chance that oldest dragonfly predators reached the final larval stage during which they strongly reduce feeding rates.

2.4 | Response variables

We monitored mesocosms daily to collect any emerging amphibian metamorphs. Only a small number of *Bufo* individuals reached metamorphosis at the end of the experiment. Metamorphs were returned to the laboratory and weighed once the tail was fully absorbed and then released at origin of capture. On the last day of the experiment, we used a depth-integrated tube sampler to take three water samples per tank. The water sample was sifted through a fine zooplankton net, and all samples were preserved in 125 ml 70% ethanol and returned to the laboratory. We identified and counted all zooplankton in a 50 ml subsample. Previous studies using the same protocol indicate that this subsampling regime accurately represents the whole 125 ml sample (Rudolf & Rasmussen, 2013a, 2013b).

At the end of the experiment, we destructively sampled mesocosms by removing all leaf litter and collecting any macro-invertebrates and tadpoles we found. Invertebrates were preserved in 70% ethanol. Tadpoles were euthanized with MS 222 before preservation. We photographed and identified all collected tadpoles and macro-invertebrates, and then dried them for 48hrs at 65°C followed by a cooling period of 48hrs in a desiccation chamber before obtaining their dry mass. We did not recover final surviving focal predators (i.e. *Cybister*) in two tanks from two different stage treatments.

All applicable institutional and national guidelines for the care and use of animals were followed and approved under IACUC protocol A13101101.

2.5 | Statistical analyses

We analysed the data in two main ways. First, we focused on each predator species in isolation to determine how species identity and stage diversity affect the functional role of predators ('*functional differences*'). Then, we tested how stage diversity influences consequences of species loss effects ('*biodiversity loss effects*').

2.5.1 | Functional differences

We used GLM with predator species treatment (A, B, C), stage diversity treatment (diverse vs. unstructured) and their interaction as fixed effects and spatial block as a random effect. A significant predator effect would indicate that predators differ in their effect on a given community metric. Similarly, a significant effect of stage diversity would indicate that effects of predators vary with population stage diversity. Finally, a significant interaction effect indicates that stage diversity had different effects for different

predators. Dry mass was always log transformed and analysed with Gaussian distributed errors and identity link function. Amphibian survival was analysed with binomial errors and log-link function. We discovered that some mesocosms had very few tadpoles of *Acris crepitans* and *Hyla versicolor*, likely introduced as eggs with benthic samples. Due to the random nature of their introduction, *Acris* and *Hyla* tadpoles were too rare to analyse their survival. However, they were included in total tadpole biomass as they consume similar resources and compete with the other two tadpole species. Overall, there was no significant difference in *Bufo* metamorph emergence among treatments, so for simplicity we only represent survival analyses based on tadpoles in main text, which showed the same pattern as analyses including metamorphs (see Tables S6 and S7; Figure S1).

Given the high diversity of zooplankton species in mesocosms, we also analysed treatment effects on zooplankton community structure. The zooplankton samples included 14 morphospecies, of which seven morphospecies were excluded from the analyses because they were too rare for a meaningful analysis (<2% of total individuals). First, we used a permutation test (function 'permanova') to test for overall treatment effects. Permutations were nested by block and based on 9,999 permutations. We then used NMDS ordination based on Bray–Curtis dissimilarity matrix to simplify community composition to quantify biodiversity loss effects.

2.5.2 | Biodiversity loss effect

To determine if and how stage diversity within populations modifies species biodiversity loss, we calculated a standardized 'biodiversity loss' effect (BLE) for each response variable as: $BLE = \ln(N_X/N_{ABC})$, where N_X is given by the response variable in treatments with only one of three predator species present ($A = Anax$, $B = Belostoma$ or $C = Cybister$) present and N_{ABC} indicates the corresponding variable in high diversity treatments with all three predators present. This metric is based on commonly used statistic to measure ecological effects in experiments (Osenberg et al., 1997) and has a clear biological meaning: for instance, $\ln(N_A/N_{ABC}) < 0$ indicates that losing *Belostoma* and *Cybister* predators from a community results in a reduction in the response variable relative to the high diversity treatment. Note, that we used differences in species diversity across communities to estimate the effect of biodiversity loss, rather than directly comparing a single community before and after a species was removed from it. While this is commonly used method in diversity studies, it assumes that absence of a species will result in the same community as the loss of a species. To measure the effect of biodiversity loss on community composition of zooplankton, we calculated the Euclidian distance between full diversity and single predator treatments within a given block along each NMDS axis. Because some values were negative for this metric, we could not use the log effect size ratio but instead used the absolute difference in the analysis.

We calculated BLE size for each block separately to account for potential block effects, resulting in five independent estimates per predator loss scenario and response variable. We then used a GLM with Gaussian error and identity link function, with predator treatment (A, B, C), stage diversity treatment (unstructured vs. diverse), response variable type and their interactions as fixed effects, and spatial block as random effect. In addition, we included mesocosm identity as random effect to account for potential non-independence of different response variables within a given mesocosm. A significant effect of stage diversity treatment would indicate that the effect of losing species diversity depends on stage structure within predator populations, and the sign and magnitude indicates whether this effect buffers or enhances consequences of species loss and by how much. Because predator loss effect had a different meaning for zooplankton community structure metrics, we repeated this analysis without those two metrics. Overall, the results were qualitatively similar, and we thus only represent the full analysis here and provide individual analysis for each metric in the supplement.

All analyses were carried out in R statistical software. We used the LME4 package (Bates et al., 2015) for all GLM analyses, and significance of the fixed predictors was determined with the 'ANOVA' function in the CAR package based on Wald chi-square statistics (Fox & Weisberg, 2011). Ordination and permutation tests for community structure were carried out with the VEGAN package (Oksanen et al., 2020). The full code for all statistical tests is available together with the data at dryad (<https://doi.org/10.5061/dryad.76hdr7sw1>).

3 | RESULTS

3.1 | Focal predator manipulation and response

While there were some species-specific differences, predator treatments were generally maintained throughout the experiment across stage diversity treatments. Survival and biomass naturally declined for all focal predators during the experiment. However, although biomass at start of the experiment was set to be similar across species, final biomass of predators differed significantly across species ($p < 0.0001$), with highest biomass for dragonflies (*Anax*) and lowest for giant water bugs (*Belostoma*) and beetles (*Cybister*; Tables S2 and S3). As expected, survival was higher for all species when alone compared to high diversity treatments when other predator species were also present ($p = 0.0001$). Depending on species identity, these patterns were driven by a reduction in per capita biomass (likely indicating competition) and/or survival (likely due to intra-guild predation; Figure 2). In contrast, final total predator biomass did not change with stage diversity treatments ($p = 0.2907$) or interactions between diversity treatments ($p = 0.8845$) or species identity ($p = 0.6482$; Table S3). Since biomass was set to be equal across treatments at the start of the experiment, this implies that any stage diversity treatment effects on prey responses were not driven by changes in predator biomass or survival.

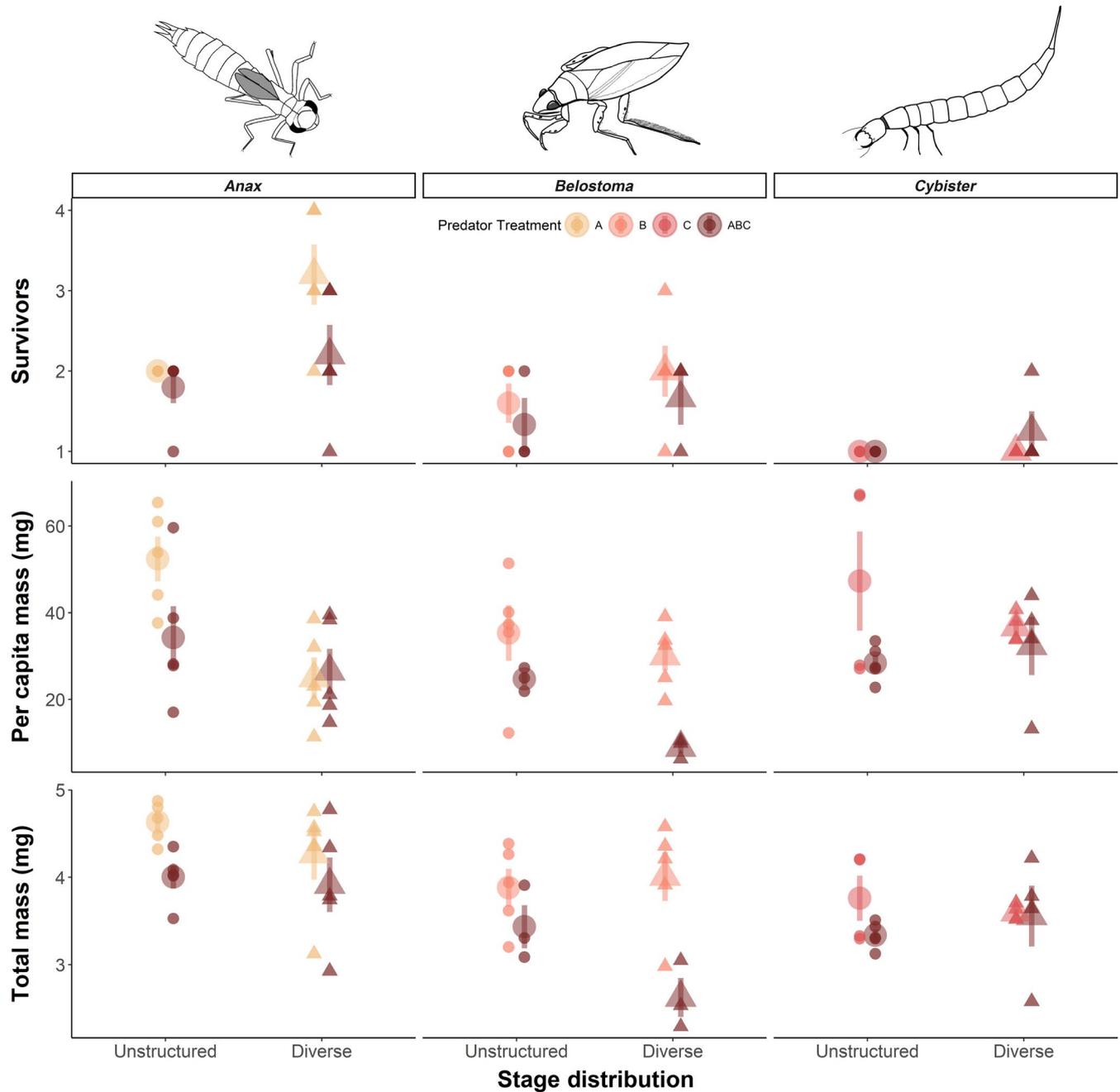


FIGURE 2 Final number of survivors, per capita mass and total mass (summed across all individuals within a predator type/mesocosm) of focal predators across stage distribution (StageDist) and predator diversity treatments. A = dragonfly *Anax junius*, B = giant water bug *Belostoma lutarium*, C = diving beetle larva *Cybister fimbriolatus*, ABC = *Anax* + *Belostoma* + *Cybister*. Small symbols indicate individual replicates and large symbols indicate average ± 1 SE for a given treatment (not accounting for block effects)

3.2 | Functional differences between predators

The functional role of predators was jointly generally determined by both species identity and population structure. As expected, predators had significantly different effects on all aspects of the prey community, except for total dry mass of macro-invertebrates (Table 1; Figures 3 and 4). For instance, dragonflies (*Anax*) had by far the strongest negative effect on total amphibian biomass and *Bufo* survival, but the smallest effect on zooplankton abundance. In contrast, the presence of diving beetles (*Cybister*) had the strongest effect on

zooplankton abundance, while giant water bugs (*Belostoma*) had no clear effect on total amphibian biomass (i.e. equal to predator-free control) and the weakest effect on *Bufo* survival. Macro-invertebrate biomass was on average lower in the presence of predators, especially with all three predators present, but did not significantly differ across predator species treatments. This lack of significance is not surprising given the high variance across mesocosms of macro-invertebrates (Figure 3) due to the very low average abundance (0–5 individuals/mesocosm/species) and high variation in presence/absence of the 49 morphospecies identified across mesocosms.

TABLE 1 Effect of species identity (PredID, *Anax junius* vs. *Belostoma* vs. *Cybister*) and stage diversity within predator populations (StageDist: unstructured vs. diverse stage distribution) on prey community. Tadpole mass, invertebrate mass and zooplankton abundance is summed across all species within the respective group. *Bufo valliceps* and *Rana clamitans* measure proportional survival in each tadpole species. Values indicate Wald chi-square statistics for a given treatment effect

Term	Tadpole mass	<i>Bufo</i> survival	<i>Rana</i> survival	Invertebrate mass	Zooplankton abundance
StageDist	0.23	0.01	0.53	0.08	3.89*
PredID	20.68***	445.81***	18.51***	2.91	9.78**
StageDist:PredID	0.69	127.68***	22.47***	1.60	0.78

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

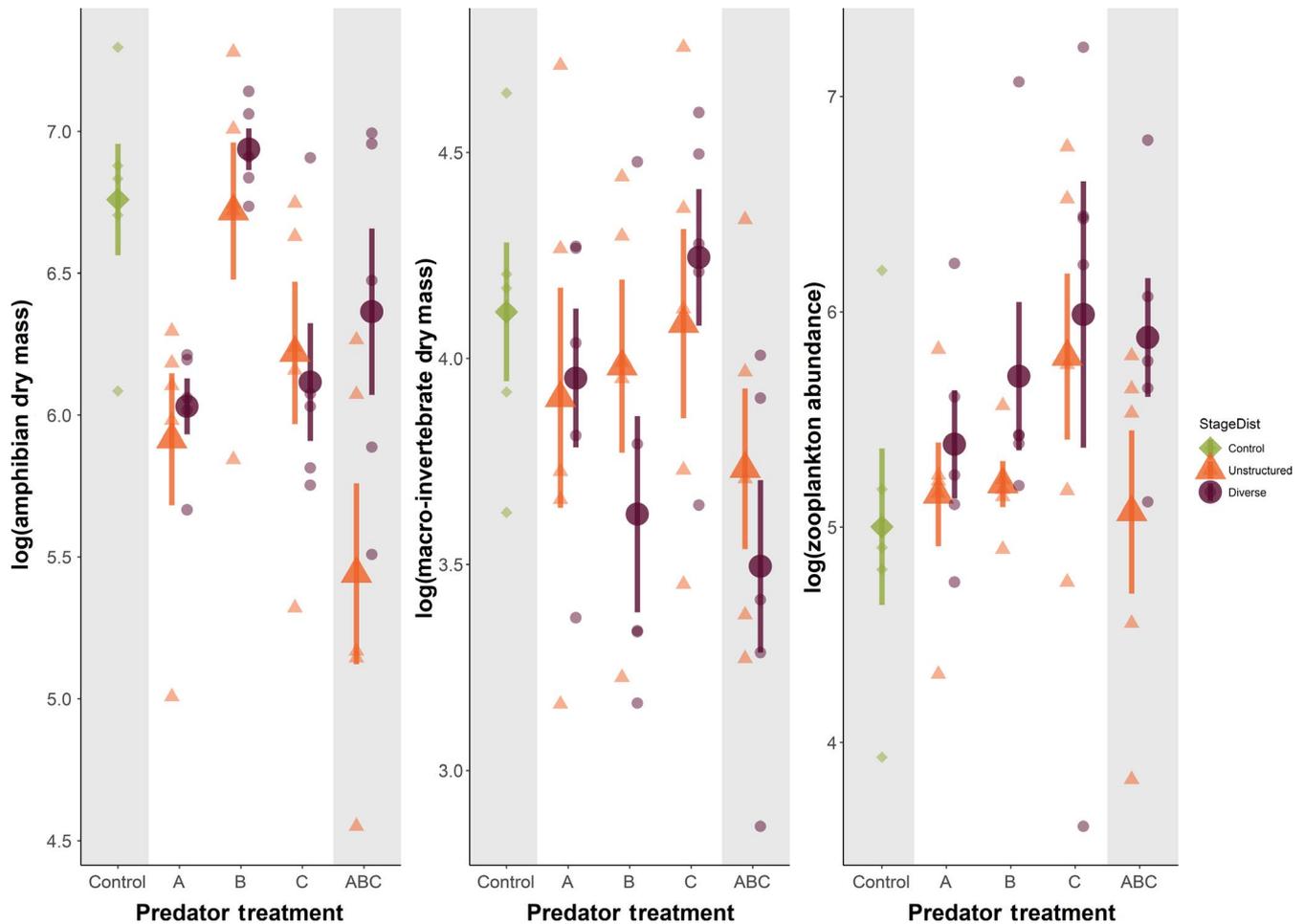


FIGURE 3 Prey responses as function of predator treatment and ontogenetic diversity (StageDist) within predator populations. Control = no focal predator, A = dragonfly *Anax junius*, B = giant water bug *Belostoma lutarium*, C = diving beetle larva *Cybister fimbriolatus*, ABC = *Anax* + *Belostoma* + *Cybister*. Small symbols indicate replicates and large symbols indicate average ± 1 SE for a given treatment (not accounting for block effects)

The effect of stage diversity within predator populations (ontogenetic diversity) was contingent on the specific response variable (Table 1). Predator stage diversity had no effect on total tadpole mass. Zooplankton abundance increased when predator populations had a diverse stage distribution compared to unstructured populations and this effect was independent of predator species identity (Figure 3). In contrast, *Bufo* and *Rana* tadpole survival was

significantly influenced by the interaction of predator identity and stage diversity (Figure 4). Dragonflies (*Anax*, A) and giant water bugs (*Belostoma*, B) had a more negative effect on *Bufo* survival when populations had low stage diversity, while diving beetle predators (*Cybister*, C) had a more negative effect when populations exhibited a diverse range of stages. Interestingly, these patterns were reversed for *Rana* tadpole survival. Overall, these results indicate

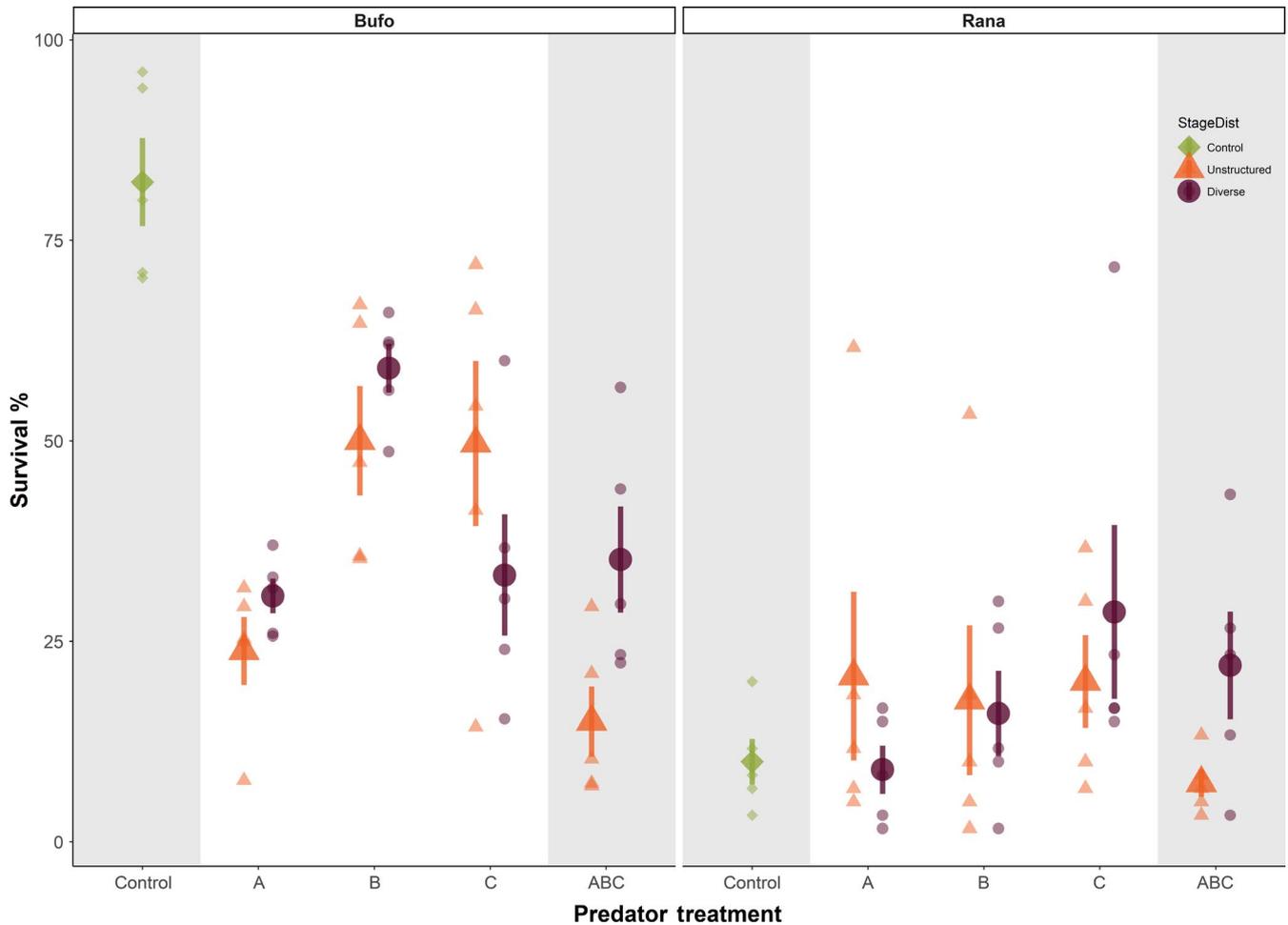


FIGURE 4 Effect of predator treatments and ontogenetic diversity (StageDist) within predator populations on survival of two tadpole species, *Bufo valliceps* and *Rana clamitans*. Control = no focal predator, A = dragonfly *Anax junius*, B = giant water bug *Belostoma lutarium*, C = diving beetle larva *Cybister fimbriolatus*, ABC = *Anax* + *Belostoma* + *Cybister*. Small symbols indicate replicates and large symbols indicate average ± 1 SE for a given treatment (not accounting for block effects)

that each predator species clearly differed in their functional roles (i.e. effect on prey community), but the effect of a given predator on the prey community was often contingent on its population stage diversity.

3.3 | Biodiversity loss effects

The consequence of losing predator species for prey community structure was significantly influenced by the size structure of predator populations (Table 2; Figure 5). Overall, losing predator diversity had a strong effect (mean BLE = 0.5, which corresponds to ~64% change) when predator populations had low ontogenetic diversity (Figure 5). With low ontogenetic diversity, lower predator diversity typically increased amphibian biomass, tadpole survival and zooplankton abundance, indicating a reduction in top-down control of the food web. In addition, reduced predator diversity in low ontogenetic diversity treatments was associated with a clear shift in zooplankton community composition (Table S9). In contrast, when predators had high ontogenetic diversity, losing

TABLE 2 Ecological factors influencing ecological consequences of species diversity loss. StageDist = ontogenetic diversity within populations (unstructured vs. diverse), Div = identity of focal predator species lost, Response = ecological (prey) response variable. See Section 2 for further details on statistical analysis and calculation of standardized biodiversity loss effect (BLE) metric

Term	Wald Chisq	df	Pr(>Chisq)
StageDist	17.95	1	0.0000
Div	5.96	2	0.0507
Response	9.85	6	0.1312
StageDist:Div	0.01	2	0.9973
StageDist:Response	15.55	6	0.0164
Div:Response	12.83	12	0.3815

Bold indicates significant values ($p < 0.05$).

predator species had on average very little consequences for the prey community (mean BLE = 0.018, ~1% change, Figure 5). For instance, communities without diving beetles (*Cybister*, C) and giant water bugs (*Belostoma*, B) had higher total amphibian

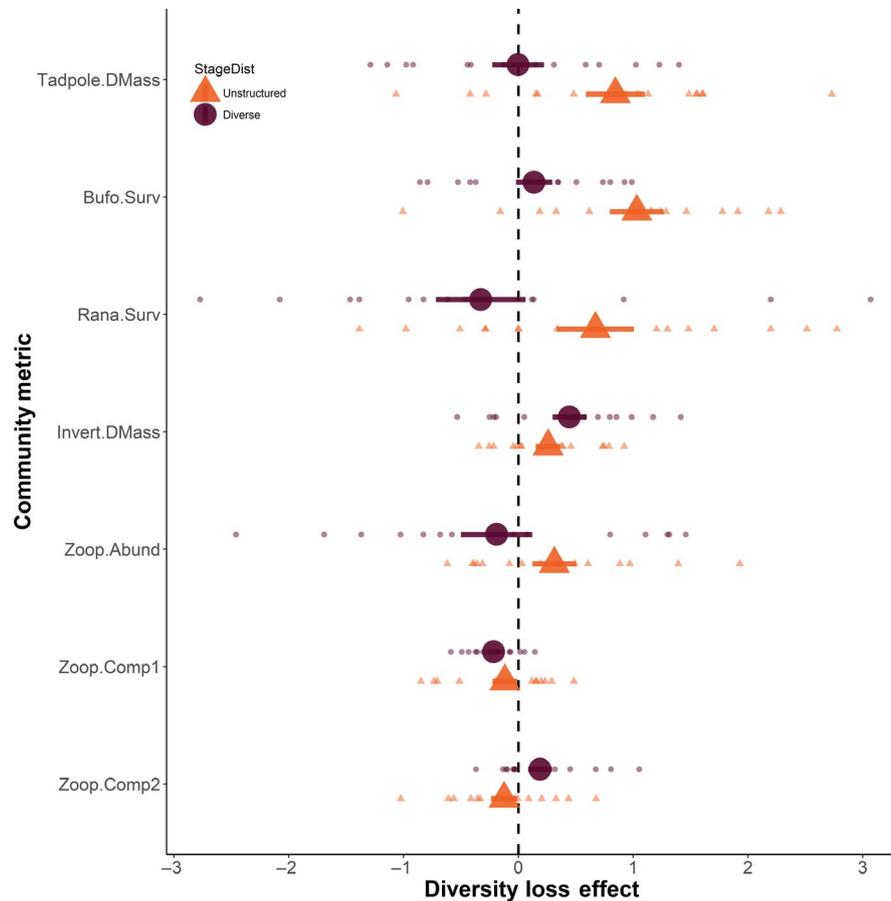


FIGURE 5 Effects of biodiversity loss on prey community. Large symbols indicate mean (± 1 SE) standardized biodiversity loss effect (BLE) for a given community metric averaged across different predator loss treatments. Positive values indicate an increase in a given metric when predators are lost from a community (see methods for BLE calculation details). Small symbols indicate raw BLE for individual replicates. Solid circles indicate unstructured predator populations (low ontogenetic diversity) and triangles represent predator populations with diverse range of stages (high ontogenetic diversity). Tadpole.DMass and Invert.DMass show change in total dry mass across all species for tadpoles and invertebrates respectively. Bufo.surv and Rana.surv show change in survival of two main tadpole species, Zoop. Abund indicates change in total abundance summed across all zooplankton species, and Zoop.Comp1 and Zoop.Comp2 indicate change in community composition, indicated by changes along the two main NMD axis (see Section 2 for details)

biomass if predator populations were unstructured, but the opposite was true when predator populations exhibit a wide stage/size distribution (Figure 3). This buffering effect of predator stage diversity was independent of which predators were lost from the community (stage diversity \times predator treatment: $p > 0.997$, Table 2). However, the magnitude of the stage diversity effect varied depending on prey response variable used (Table 2; Figure 5; Tables S5, S8 and S10). The strongest buffering was observed for amphibian response variables, while this effect was weak or absent for zooplankton abundance and macro-invertebrate biomass. The latter pattern was largely driven by the simple fact that macro-invertebrates and total zooplankton biomass were too variable across mesocosms to detect any clear predator effects in our experiment (Table S8). An overall marginal species identity effect (Table 2) suggests that it still mattered which predator species was lost. This effect largely reflects the differences among predators outlined above and was much less important for the diversity loss effects than the stage diversity within predator populations.

4 | DISCUSSION

While the ecological importance of intraspecific variation is increasingly appreciated (Bolnick et al., 2011; Dibble & Rudolf, 2019; Hughes et al., 2008; Violle et al., 2012), previous studies have largely focused on ontogenetic niche shifts, genetic variation or ecotypes within a single focal species (Des Roches et al., 2018; Raffard et al., 2019). As a consequence, the potential interactions of intraspecific diversity and taxonomic diversity are still not well-understood (Raffard et al., 2019). We found that the diversity of developmental stages within populations (ontogenetic diversity) influenced the functional role of species, and thus the biodiversity patterns at higher organizational levels. Furthermore, we demonstrate that ontogenetic diversity can also buffer communities against the consequences of taxonomic diversity loss for some, but not all community metrics. Together, these results provide new insights into the importance of ontogenetic diversity for the resilience of natural communities to biodiversity loss and emphasize

the need to measure and account for biodiversity across different organizational scales.

4.1 | Ontogenetic functional diversity

At the population scale, diversity is driven by trait variation across individuals within species. Although ontogenetic niche shifts are ubiquitous key drivers of individual variation in natural populations (De Roos & Persson, 2013; Miller & Rudolf, 2011; Nakazawa, 2015; Rudolf, 2020; Rudolf & Lafferty, 2011; Werner & Gilliam, 1984), we still have a limited understanding of how they scale up to influence the functional roles of species, especially when stages co-occur. We found that species identity and ontogenetic diversity within populations jointly determined the ecological impact of a predator species. The strong effect of species identity is not surprising, given that each species represents a unique taxonomic order, with very different morphologies, habitat use, feeding mode and behaviour. Our results are consistent with previous studies, confirming that *Anax* and *Cybister* are important generalist predators, and more effective at controlling tadpoles than *Belostoma*. Furthermore, we were able to show that the effects (magnitude and even direction) of a given predator species on the community was contingent on the stage distribution within predator populations and vice versa. For instance, increasing stage diversity could have a positive or a negative effect on a given prey depending on the predator species (e.g. increasing stage diversity in *Cybister* decreased *Bufo* survival while the opposite was true for *Anax*). Similarly, increasing stage diversity had a positive effect on one metric and a negative effect on another (e.g. *Rana* vs. *Bufo* survival).

While these context-dependent effects may seem idiosyncratic, they are consistent with recent experiments which found that size effects are often species specific, even when species are within the same taxonomic family (Rudolf & Rasmussen, 2013b; Rudolf et al., 2014). Species-specific ontogenetic diversity effects arise because size alone cannot capture all the differences in traits (e.g. morphology, feeding mode, habitat use) and concurrent ecological interactions of individuals across species (Rudolf et al., 2014). A recent meta-analysis found that intraspecific diversity effects generally vary across species (Raffard et al., 2019), suggesting that species-specific effects of intraspecific diversity are common. Unfortunately, for biodiversity studies in complex and diverse systems like ours (>14 zooplankton species, >43 macro-invertebrates and four tadpole species), it is impossible to determine what exact direct and indirect interaction pathways and species traits determine these differences across and within predator species. However, regardless of the specific underlying pathways, these results confirm that neither taxonomic identity nor size alone is sufficient to predict the functional role of individuals in a community (Rudolf et al., 2014). Instead, we need to embrace a trait-based approach that accounts for both species-specific constraints and changes in traits and ecological interactions over ontogeny. Size is often a good trait to capture individual functional differences within species

(Woodward et al., 2011; Woodward & Hildrew, 2002), but size effects are often species specific (Rudolf et al., 2014), likely due to differences in species-specific traits (e.g. foraging mode, habitat use, morphology; Klecka & Boukal, 2013). Combining species and trait-based approaches thus could be an important step forward towards more accurately capturing functional differences within and across species.

4.2 | Biodiversity loss

Biodiversity loss typically leads to concurrent changes in ecosystem processes, but the quality and quantity of these changes can vary across studies and systems (van der Plas, 2019). This variation is often attributed to differences in environmental conditions, composition of communities or identity of species lost. Here, we found that diversity of stages/size within the species buffered against the loss of taxonomic diversity for four out of seven community response metrics. This indicates that even if all environmental conditions are similar, differences in the intrinsic structure of populations can modify the consequences of biodiversity loss. It also suggests that previous experimental studies that used unstructured populations may overestimate the consequences of biodiversity, emphasizing the need to accounting for natural size/stage variation within populations in biodiversity studies.

The buffering effect of ontogenetic diversity is likely driven by several non-exclusive mechanisms. Biodiversity can buffer against species loss when it increases the functional overlap of species. Consequently, if increasing ontogenetic diversity decreases functional differences between species, this could help buffer against species loss from the community. We found that ecological differences between species were generally smaller when populations had high ontogenetic diversity. For instance, dragonflies and diving beetles had more similar effects on amphibian biomass when populations had wide stage range than unstructured populations. Importantly, an increase in functional similarity also implies that the identity of the species lost from a system should be less important. This prediction is consistent with our result that losing diving beetles or dragonflies had the same effect when populations had high stage diversity, but not in unstructured populations.

Besides functional overlap, network complexity and the potential for indirect interactions are also known to buffer against biodiversity loss (Cardinale et al., 2012; Duffy et al., 2007). Predation is generally highly size specific, with larger individuals consuming smaller individuals. Increasing stage diversity within our focal predator therefore also increased the potential for predation within (cannibalism) and between species (intra-guild predation) in this system (Carter et al., 2018). Thus, network complexity and potential for indirect interactions is increased with ontogenetic diversity, which can modify the effect of individual species on the ecosystem.

Indirect interactions can be mediated by changes in density (numerical effect) and per capita effects. When a predator consumes

other predators that also share the same prey (intra-guild predation), losing that predator from the system can increase the density of remaining predators which could in turn can at least partially compensate for the loss of a predator (Crumrine, 2010; Denno et al., 2004; Griffen & Byers, 2006). If this mechanism is responsible for buffering species loss, we would expect to see lower biomass in size-structured treatment compared to unstructured treatments, especially at high predator diversity. While we did see a general decline in survival of the different predator species in high versus low diversity treatment (indicating intra-guild competition and/or predation), we did not find a significant effect of size-diversity treatment on final total biomass of predators, regardless of whether species were alone or together with other predator species. Thus, the ontogenetic diversity effects were likely driven by changes in per capita effects of individuals. For instance, individuals often forage less in the presence of a potential predator, and/or switch diet and micro-habitat use (non-consumptive indirect effects or trait-mediated indirect effects; Rudolf, 2006; Rudolf & Armstrong, 2008). In this scenario, removing a predator can increase the per capita effect of remaining predators on the prey community, thereby compensating for the predator loss. The strength of these non-consumptive buffering effects should increase with increasing size differences between individuals (Krenek & Rudolf, 2014). Consistent with this prediction, removing either dragonfly (*Anax*) or diving beetle (*Cybister*) predators from the system had little consequences for amphibian biomass in size-structured populations in this study. In contrast, amphibian biomass increased substantially in unstructured predator population treatments, especially when *Anax* was lost. Interestingly, stage diversity had no effect when dragonflies or diving beetles were alone, suggesting that this buffering effect of ontogenetic diversity was largely driven by size-structured non-consumptive effects across species rather than within species. However, for other community metrics (e.g. zooplankton abundance, *Bufo* survival), size-structure treatments also determined the effect of a given species, indicating that the buffering effect of ontogenetic diversity could be driven by both, intraspecific and interspecific non-consumptive indirect interactions.

It is important to keep in mind that intraspecific diversity per se does not necessarily have to be important or positive. Here we focused on apex predators, and effects may be less noticeable in other community members. Furthermore, whether effects of intraspecific variation are positive or negative should depend on the ecological context, that is, on phenotype-environment matching (Dibble & Rudolf, 2019), which includes community structure. For instance, genetic diversity can have negative consequences for populations in more diverse communities (Hahn et al., 2017). Ultimately, the interaction of intraspecific diversity and biodiversity loss should depend on how diversity within species influence interactions and ecological differences between functional groups. Thus, to better integrate biodiversity across organizational scale, we need to know more on how functional differences between species vary over their ontogeny across species and ecosystems.

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AUTHORS' CONTRIBUTIONS

V.H.W.R. designed the study and analysed the data; V.H.W.R. and L.E. conducted the experiment and wrote the manuscript.

DATA AVAILABILITY STATEMENT

All the data including R codes are publicly available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.76hdr7sw1> (Rudolf & Eveland, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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