nature ecology & evolution

ARTICLES

PUBLISHED: 13 JANUARY 2017 | VOLUME: 1 | ARTICLE NUMBER: 0038

Legacy effects of developmental stages determine the functional role of predators

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Predators are instrumental in structuring natural communities and ecosystem processes. The strong effects of predators are often attributed to their high trophic position in the food web. However, most predators have to grow and move up the food chain before reaching their final trophic position, and during this developmental process their traits, interactions and abundances change. Here, we show that this process of 'moving up' the food chain during development strongly determines the ecological role of a predator. By experimentally manipulating the succession of developmental stages of a predatory salamander in a seasonal aquatic ecosystem, we found that the effects of this apex predator on the ecosystem typically declined with age and size. Furthermore, younger, smaller predator stages had long-lasting effects on community structure and ecosystem function that determined the effects of subsequent older, larger stages. Consequently, the legacy effects of early stages largely shaped the impact of the predator on the ecosystem, which could not simply be inferred from its final trophic position. Our results highlight that accounting for all life stages when managing natural populations is crucial to preserve the functioning of natural ecosystems, especially given that early life stages of species are often particularly vulnerable to natural and anthropogenic disturbances.

Anthropogenic activities are driving changes in the abundance and presence of species worldwide[1–3]. Whether and how these changes influence the rest of the community and ecosystem processes depends on the functional role of the species[2,4]. Early on, ecologists recognized that not all species are equal; instead, some species, such as keystone or apex predators, can have disproportionally strong impacts on ecosystem functioning by shaping community structure[5,6]. However, what traits determine the key role of these predators on the ecosystem remains controversial. For instance, the traditional view suggests that the disproportional effects of apex predators on the ecosystem arise because these species are at the top of the trophic food chain[1,5]. However, this view is typically derived from species-based food webs, which ignore that most individuals (except for some mammals and birds with prolonged parental care) are not typically born into their final trophic position. Instead, predators such as sharks and other predatory fish, reptiles, amphibians and most invertebrates have to grow and develop while moving up the food chain before reaching their final trophic position. During this developmental process (ontogeny), their traits, ecological interactions, abundances and thus their functional roles, change[7–12]. The final trophic position of a predator may therefore represent only the last 'snapshot' of a long series of changing ecological interactions, but whether this final snapshot is representative of the functional role and importance of a species remains to be tested.

Here we hypothesize that accounting for 'historical' interactions that occur during the ontogeny of species is crucial to determine the impact of individuals and species on the ecosystem. Just as we often cannot predict the current state of a community without accounting for what species were present in the past ('ghost species')[13,14], the current functional role (that is, effect on community structure and ecosystem processes) of a species should depend on its 'historical' interactions in the ecosystem. At every step of their development, individuals can alter and shape community structure and ecosystem processes. If these effects persist after a stage is gone, an individual can only encounter and influence a world that has been previously shaped by its former self. Such 'ontogenetic' legacy effects could lead to non-independence (non-additive effects) of developmental stages, and we could not predict the effect of a species (or a given individual) on the ecosystem by its final trophic position without accounting for how it has shaped the community over its entire life cycle.

We took a new experimental approach to examine how the history of interactions determines the functional role of an apex predator. Specifically, we manipulated the succession of developmental stages in the predatory salamander, *Ambystoma talpoideum*, in seasonal pond communities to test how the individual and combined effects of subsequent developmental stages affect community structure, ecosystem processes and ultimately the functional roles of a species. To identify the relative and their interactive effect of developmental stages on community structure and ecosystem processes, we used $2 \times 2 \times 2$ full factorial design that manipulated the presence or absence of successive ontogenetic stages of *A. talpoideum* in experimental ponds at three different times during their development (Fig. 1). These treatments resulted in eight types of community that differed in their history with respect to the succession of ontogenetic stages of an apex predator. Each of the three ontogenetic periods (PI, PII, PIII) was more than 4 weeks (that is, 30–31 days) long and together they covered most of the larval period of *A. talpoideum*. Predators were introduced to a set of complex experimental pond communities in 1,000l mesocosms that closely mimicked the natural habitat of *A. talpoideum*, harbouring >57 morphospecies from a wide range of taxa, functional groups and size classes (see Supplementary Information for details on experimental pond communities). Analyses of ten key ecosystem variables, including ecosystem processes such as primary productivity and community structure based on 257,522 individuals from >57 morphospecies, revealed that ontogenetic legacy effects of stages were indeed common, long lasting and modified the community that subsequent stages encountered. These results emphasize the importance of indirect feedback loops between developmental changes of predators

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through the community, and suggest that we often cannot infer the impact of apex predators on natural ecosystems from their final trophic position without considering their developmental history.

Results

Overall, we found substantial differences across predator treatments for all ecosystem responses (Table 1). Importantly, we found that the impact of earlier stages on the ecosystem persisted long after they were gone. This altered how communities changed over time and the effects of subsequent stages (Table 1, Figs 2–4). These results indicate that the focal predator strongly influenced the structure and functioning of the ecosystem, and highlight that early stages and historical contingencies strongly determine how a predator species shapes an entire ecosystem.

The final predator stage is commonly assumed to have the strongest impact on an ecosystem because it has the highest trophic position and the strongest per capita effect[15]. In contrast, we found that early and intermediate stages typically had a stronger effect on community structure and ecosystem processes than the final developmental stage. The first two predator stages influenced all measured ecosystem variables (from composition and total biomass of functional groups to net primary productivity) while they were present in a community (that is, during PI and PII, respectively). In comparison, the final, largest predator stage had much weaker effects while present (during PIII), and in some cases it had no significant effects on functional groups or ecosystem processes, such as amphibians, benthic algae (periphyton) and respiration rates (Figs 2–4, Table 1).

Effects of early and intermediate stages had long-lasting effects on all aspects of the ecosystem, from the composition and final biomass of functional groups to ecosystem processes (Table 1, Fig. 2, Supplementary Fig. 1). Importantly, effects of early predator stages not only persisted but sometimes even increased over time, frequently rivalling or exceeding the effects of subsequent predator stages that were actually present during a given time period. For instance, early predator stages had by far the strongest effect on the composition of zooplankton communities at the end of the experiment (Fig. 2), and the first two stages had stronger effects on total biomass of amphibians and final macro-invertebrates, and decomposition rates, than the last predator stages (Fig. 3, Supplementary Table 1, Supplementary Fig. 1). This striking pattern was robust and remained after we corrected for differences in relative biomass across predator stages. The per unit biomass effect of predators on decomposition rates was still on average five to nine times stronger in treatments with only early or intermediate stages present than in treatments with only late predator stages. The same general pattern was true for total amphibian biomass and final macro-invertebrate biomass (see Methods). Importantly, because stage effects were often qualitatively opposite between earlier and late stages (relative to their predator-free controls), the results are robust to potential differences in biomass, growth rates or metabolic rates across stages. Finally, treatments with all three stages present had by far the highest total predator biomass but never the strongest effect, indicating that predator effects on the ecosystem do not simply scale with total predator biomass. Overall, these results clearly indicate that predators did not become more important at the end of their development as often assumed. In contrast, they started to produce long-lasting impacts on the structure of the ecosystem from day one, and their effects declined during later stages.

One of the most striking patterns we found was that effects of intermediate and late predator stages were typically contingent on the presence of previous stages, leading to frequent non-additive effects of subsequent stages (Table 1). For instance, the effect of intermediate stages on all ecosystem processes measured at the end of PII was always contingent on whether early predator stages had been present or absent previously (Table 1). Similar non-additive

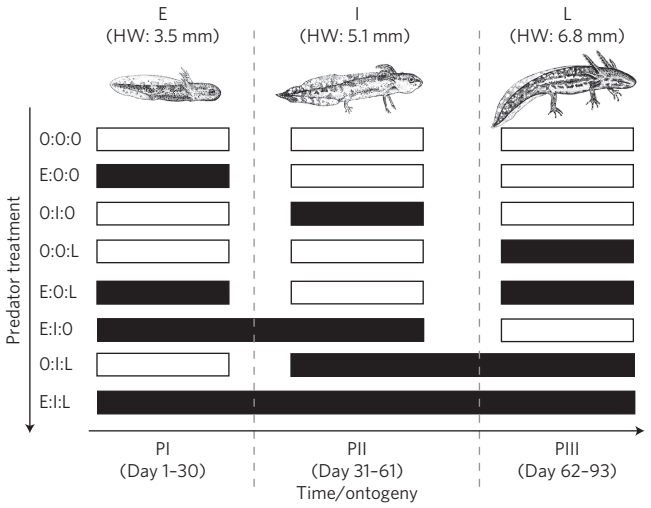

Figure 1 | Treatments manipulating the succession of predator stages. The experiment manipulated the presence (filled bars) and absence (open bars) of successive ontogenetic stages of the apex predator *A. talpoideum* by removing or adding stages in a full factorial design. Head width (HW) indicates the starting size of individuals at a given stage. Note that each stage could only occur during its respective period (E→PI, I→PII, L→PIII) and the duration of each stage was the same. 0 = predator-free control. Salamander illustrations by A. E. Dunham.

effects emerged between intermediate and late predator stages. While this interaction was not significant for periphyton and macro-invertebrates (Table 1), the lack of significance in these two cases simply stems from the fact that late predator stages had no detectable effect (Figs 2 and 3). Finally, the significant three-way interaction between early, intermediate and late predator stages on total macro-invertebrate biomass at the end of the experiment (Fig. 4, Supplementary Table 1) highlights that ontogenetic legacy effects can last for long time periods and lead to non-additive effects across several predator stages.

Discussion

Predators are typically not born into their final trophic position; instead, individuals grow and develop while moving up the food chain[7,10,11,15,16] and the final trophic position represents only the last 'snapshot' of a long series of changing ecological interactions. Our results demonstrate that effects of early predator stages on the ecosystem can rival or exceed effects of final predator stages. Moreover, we show that 'historical' interactions occurring during earlier developmental stages of a predator have long-lasting effects and change the environment encountered by subsequent stages. As a consequence, effects of later predator stages were typically contingent on the presence of previous stages, leading to non-additive effects of successive developmental stages. Our findings thus challenge current approaches by demonstrating that we often cannot infer the functional roles of a species using temporal (developmental) 'snapshots' without accounting for how it has shaped the community during earlier life stages. Given that the vast majority of species, from plants to apex predators, go through a succession of ecological changes during their development, our results are likely to apply to a broad range of species and ecosystems.

Our results highlight the challenge of predicting which predator stage (or combination of stages) has the strongest effect on an ecosystem[7,8,17,18]. While size, and thus per capita consumption rate, typically increases during the ontogeny of a predator, population density naturally decreases as well[15,19]. Furthermore, ecological interactions typically change substantially during ontogeny, leading to low resource overlap across developmental stages[9,16], especially

Table 1 | Effects of predator stage succession on ecosystem properties over time.

	Community structure of functional groups								
	Zooplankton			Macro-invertebrates			Amphibians		
Predator stages	PI	PII	PIII	PI	PII	PIII	PI	PII	PIII
E	13.05**	3.41*	1.03	32.79***	6.41***	1.22		39.46***	2.99*
I		7.27**	0.63		3.70***	1.7*		8.18**	5.28**
E × I		2.59*	2.33†		0.68	1.11		5.78*	2.80†
L			0.42			0.57			0.29
E × L			0.67			0.50			0.57
I × L			3.94**			0.29			3.65*
E × I × L			0.93			0.45			0.01

	Ecosystem rate							Primary producer biomass					
	k	NPP			Respiration			Periphyton			Phytoplankton		
Predator stages	PIII	PI	PII	PIII	PI	PII	PIII	PI	PII	PIII	PI	PII	PIII
E	8.38**	4.07*	1.06†	0.07	3.93*	7.81**	1.08	8.81**	3.92*	1.78	5.64*	0.01	1.13
I	8.21**		0.49	1.27		2.43	0.10		4.24*	2.42		0.03	0.40
E × I	0.01		5.23*	0.48†		7.07**	0.79		7.38**	2.60		0.87	0.09
L	0.01			3.42			0.20			0.62			0.04
E × L	0.22			0.16			0.29			0.86			0.69
I × L	0.03			4.52*			1.73			0.52			3.05†
E × I × L	0.34			0.45‡			0.08‡			1.14			0.06

**$P \leq 0.01$, *$P \leq 0.05$, †$P < 0.1$. ‡Non-significant ($P > 0.5$) term was dropped for final analysis of other factors. Community structure, NPP, respiration and primary producer biomass were analysed based on subsamples collected at the end of each of three consecutive periods (PI: day 1–30; PII: day 31–61; PIII: day 62–92; see Fig. 1), whereas decomposition could only be estimated after the final period. Note that early (E), intermediate (I) and late (L) predator stages were only present during PI, PII and PIII, respectively. Thus, significant effects of early and intermediate predator stages during later periods when they were absent indicate ontogenetic legacy effects. Community structure was analysed with a multivariate permutation test (PERMANOVA) using proportional abundances of species, and ecosystem processes and primary producer biomass with GLMM with respective error structure. All analyses included block as random effect (see Supplementary Information for details). Community structure shows pseudo *F*-statistics, whereas ecosystem rates and biomass are chi-squared statistics.

when considering the dramatic changes in community structure over time that can occur independently of the predator[16,20]. A similar pattern was present in our system: because of natural seasonal shifts in species composition in our system, zooplankton, macro-invertebrate and amphibian communities were dramatically different between PI and PIII, even within the predator-free control. Because of these changes in food web configurations across stages and time periods, we argue that there is no a priori reason to expect effects of different developmental stages simply to scale with per capita or biomass effects, or trophic position[7,8,12]. Indeed, even after correcting for differences in total predator biomass, the patterns in our results remain robust. This is consistent with previous studies suggesting that keystone species can occur at all trophic levels[6]. Our results thus challenge the commonly held view that larger predators with higher trophic positions are more important; instead, early stages can be just as or even more important in driving community structure and ecosystem processes than later developmental stages, and need to be considered when managing natural populations and ecosystems.

Several factors could drive differences in the effect of predator stages. Community composition naturally changed over the season and became more diverse over time. Late predator stages encountered a more variable and more diverse community, and thus were embedded in a more complex food web. This complexity could lead to more weak/diffuse interactions and thereby reduce per capita interaction strength of late predators. Furthermore, higher food web complexity provides more opportunity for indirect interactions and compensatory responses among prey species compared with simpler communities during earlier periods. However, the stronger effect of early stages is still surprising, given that early predator stages encountered a much smaller pool of the available prey and for a shorter time period than intermediate or late predator stages. For instance, the first predator stage could only interact for less than 2 weeks with a very small fraction of tadpoles (82 out of 467) from only two of the four tadpole species (*Pseudacris triseriata* and *Hyla versicolor*). In contrast, the largest tadpole additions occurred early during the final period. Yet, early predator stages had a much stronger effect on total amphibian biomass produced by a given mesocosm than late stages (Supplementary Table 1). Similarly, early stages had a strong effect on final zooplankton and macro-invertebrates, even though they did not encounter many of these species and many of the prey species completed multiple generations after early stages were gone.

The strong, long-lasting effect of early stages on the final community composition indicates that these effects led to a cascade of complex indirect interactions over time. Changes in the structure of communities during early colonization periods often lead to long-lasting differences in community composition because they can alter the relative performance of species that arrive later[21–24]. Such historical contingencies (or priority effects)[24] could also explain the patterns we observed in our system. For instance, early stages dramatically reduced the density of *P. triseriata* tadpoles during PI, which was in turn negatively correlated with the density of *Bufo nebulifer* tadpoles during PII, suggesting strong indirect interactions between early predator stages and *B. nebulifer* during PII. Similarly, intermediate stages prevented successful colonization of the highly predatory dragonfly *Pantala flavescens* (probably by eating the dragonflies shortly after they hatched) during PII, which strongly influenced macro-invertebrate biomass (see Supplement). Thus, the long-lasting effect of earlier developmental stages of our focal predator was mediated by a series of indirect interactions that

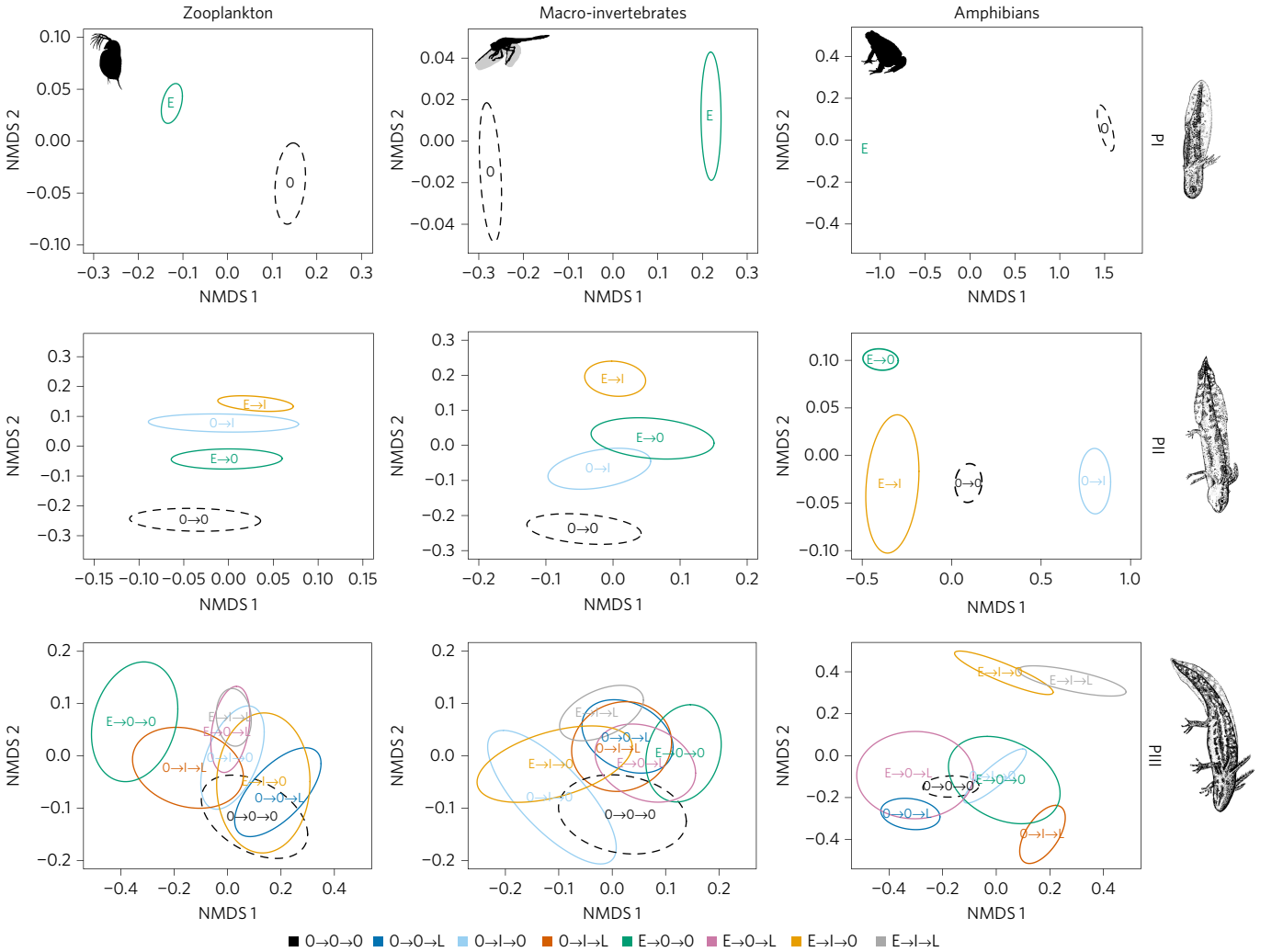

Figure 2 | Differences in composition of macro-invertebrates, amphibians and zooplankton across three predator time periods, PI–PIII (see Fig. 1). Ordination plots show mean ± 1 s.e.m. standard ellipse based on abundances of species at the end of a given time period, and include metamorphs during that time period for amphibians. Note that standard ellipses are based on raw data and do not account for significant block effects in Table 1 and thus only approximate actual differences. E, early stage was present; I, intermediate stage was present; L, late stage was present; 0, predator-free control during a respective time period. Note that because of large seasonal transitions in community composition, the axes are different across periods and functional groups. For amphibians, the E treatment ellipse is small and hidden behind the centroid label. Colours represent different predator treatments across periods indicated in the key. Salamander illustrations by A. E. Dunham.

cascaded through the food web over time and altered subsequent species interactions and their relative fitness.

This cascading priority effect of early stages could also help explain the stronger effect of earlier stages on final ecosystem processes such as total amphibian biomass or decomposition rates. Early stages had the opportunity to influence the ecosystem at a much earlier stage and these effects continued to shape the ecosystem over time. The experiment ended after PIII because natural salamander ponds typically dry out soon after salamanders reach metamorphosis, and because we had to sample destructively to measure ecosystem variables. Thus, although late stages had more available prey, they could only affect the system while present but not subsequently like early stages. However, this temporal cascade mechanism cannot explain why the effects of early and intermediate stages were stronger relative to the matching predator-free control while they were present (for example, effect size (relative to matching control) of early stage during PI versus late stage during PIII). Importantly, these various mechanisms (for example, difference in complexity and arrival order) simply reflect the natural biology of many seasonal (non-stationary) systems. Together, our results indicate that the stronger effects of early stages relative to late stages were driven by differences in the direct and indirect ecological interactions of stages, and demonstrate how important early developmental stages can be in driving the dynamics of such complex communities.

Our results highlight an important issue: we could not predict the effect of a given predator stage on the ecosystem without accounting for how earlier developmental stages have shaped the community in the past. Individuals can only influence the environment they encounter. Our results demonstrate that the environment that intermediate and late predator stages encountered was already heavily shaped and changed by their former selves. These changes in the environment are likely to alter the net effect of a predator on the community. For instance, intermediate predators could consume only prey (for example, *P. triseriata* tadpoles) that actually survived PI. Such functional 'redundancies' of subsequent stages help explain many of the non-additive effects in our study where the combined effects of two stages were less than expected based on their individual effect. However, our results also demonstrate that the

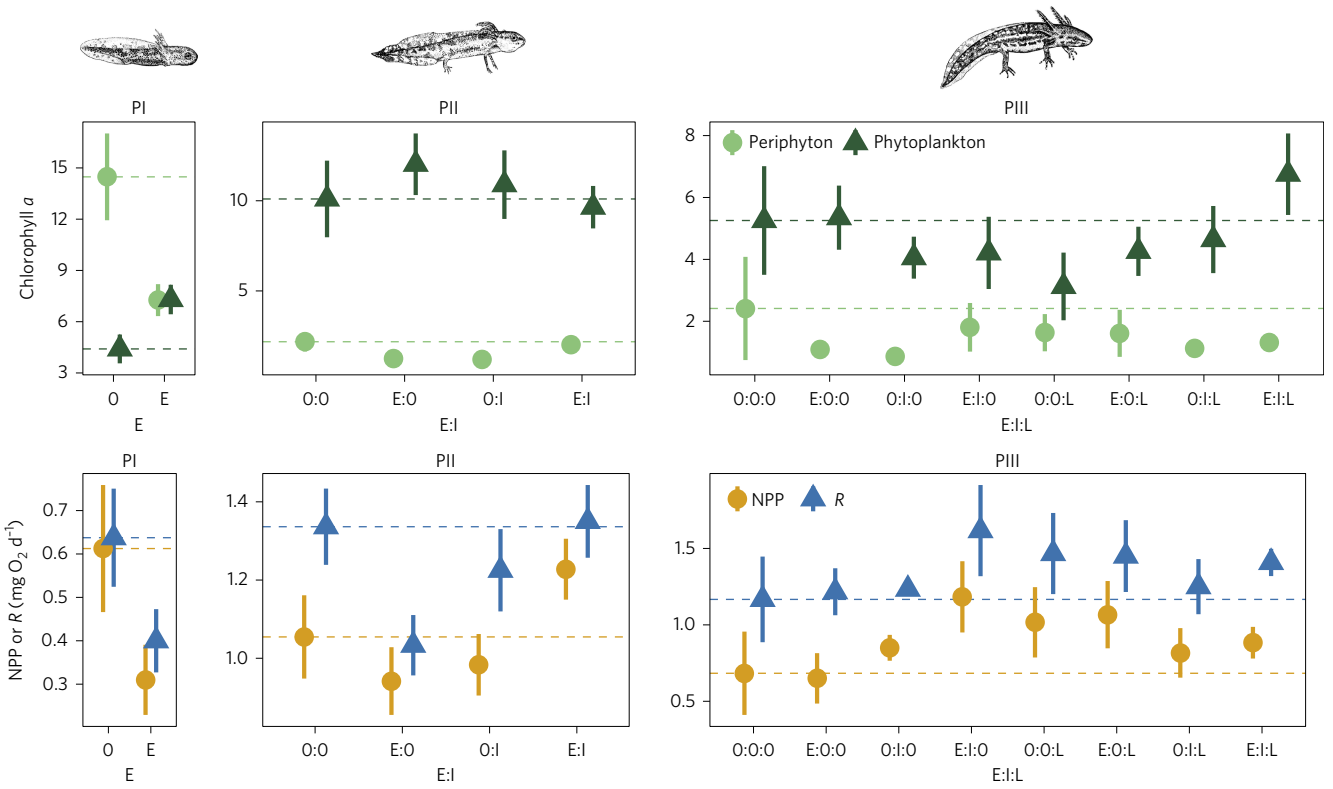

Figure 3 | Change in mean (±1 s.e.m.) abundance of two types (benthic algae: periphyton; pelagic algae: phytoplankton) of primary producer (top panels), and NPP and *R* over time as a function of predator stage sequence history (bottom panels). Estimates are based on subsamples at the end of each period. Algae abundance was estimated from chlorophyll *a* concentration either as mg ml^{-1} (phytoplankton) or mg cm^{-2} (periphyton). Note that during PI, PII and PIII, only predator stage E, I or L was present, respectively. So the effects of E or I during later periods indicates ontogenetic legacy effects. Predator treatment indicates the predation history of a given treatment with 0 indicating the absence of a given predator stage during a given time period (see Fig. 1 for details). Dashed lines indicate predator-free control mean for reference. Means and s.e.m. values do not account for significant block effects, which are included in the GLMM analyses in Table 1. Primary producer biomass is based on chlorophyll *a* concentration. Salamander illustrations by A. E. Dunham.

temporal separation of stages can lead to important synergistic effects of stages. For instance, the presence of only early or late stages reduced net primary productivity (NPP) relative to the predator-free control at the end of PII, while the opposite (that is, NPP was higher than control) was true when both stages were present in sequence. In our system, tadpoles are negatively correlated with NPP because they reduce oxygen (via respiration) and they consume primary producers (periphyton)[7,12]. On their own, early and intermediate predator stages could regulate tadpoles during only one period, leaving one time period during which tadpoles could strongly reduce periphyton and NPP rates. However, when both stages were present, they could regulate tadpole densities during both time periods, allowing periphyton and hence NPP to increase. Thus, the temporal separation of stages created important complementary functional differences between both predator stages. Note that our design prevented any carry-over effects (from one stage to the next) in the focal predator (for example, morphology or behaviour) itself (see Methods) by mixing and randomizing predators across treatments between each period. Although we could not always identify the exact underlying mechanisms for all responses due to the high complexity of our study system, all non-additive effects of predator stages have to be linked to similar changes in community structure.

The ontogenetic legacy effects and associated non-additive effects of developmental stages observed in our study can always emerge when individuals shape the environment around them while they grow and develop[25]. Thus ontogenetic legacy effects are likely to be common in a wide range of systems and could help explain patterns in field studies where changes in densities of early stages reduced performance of later stages, probably because of the changes in the ecosystem mediated by early stages[25]. Although likely to be common, the importance of legacy effects should vary depending on the specific system and we expect them to have the strongest effects in species with pronounced cohort dynamics (for example, seasonal communities) where multiple stages inhabit the same environments and have strong impacts on the ecosystem. Given that the vast majority of organisms experience ontogenetic niche shifts and at least to some extent shape their environment, these results should apply to a diverse range of taxa and systems, ranging from plants to animals and aquatic to terrestrial systems.

The ontogenetic legacy effects in our study highlight a new problem for biodiversity studies: how can we predict the impact of a species on the ecosystem while accounting for such historical contingencies? To answer this question, we suggest that we need to move away from the traditional static 'black box' approach (such as Lotka–Volterra-type food web models) in community ecology that assumes that the functional role of individuals is constant over time, and instead take a temporally explicit approach that accounts for changes in the functional roles across developmental stages[26]. For example, experiments examining only one (for example, the last) stage of an apex predator will find a certain effect, but this effect may not explain what actually happens in natural systems because it does not account for the natural legacy effects of previous stages.

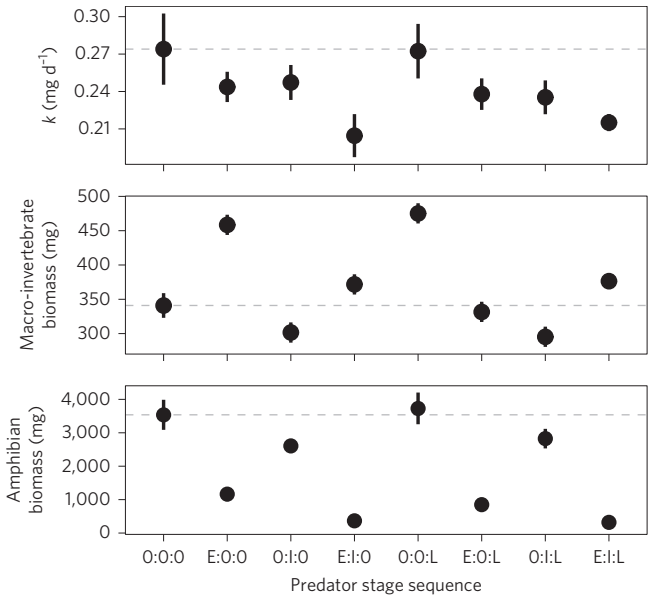

Figure 4 | Effect of predator stage sequence on mean (±1 s.e.m.) decomposition rate *k*, final macro-invertebrate biomass and total amphibian biomass. Biomass is based on dry weight summed across all species in a functional group and includes individuals that emerged during the experiment and individuals left at the end of the experiment. Dashed lines indicate predator-free control means for reference. For further details see Methods. Note that for simplicity, figures do not include significant block effects and covariates, which are included in analyses in Table 1. Predator stage sequence indicates presence/absence of E, I and L predator stages during PI, PII and PIII, respectively; 0, absence of a given predator.

The legacy effects could thus also help explain when laboratory experiments are not consistent with field studies.

Recent studies have made great strides in identifying the factors driving historical contingencies in community assembly by explicitly focusing on transient dynamics and shifts in species interactions[21,24,27–30]. Many of the same principles could apply to ontogenetic legacy effects within species, with the important exception that unlike species, developmental stages are not independent units, that is, they are inherently linked to each other through reproduction and development. For instance, any factor that changes the density (such as an increase in mortality) of early stages will also inherently affect the abundance of later developmental stages. In our case, we did not find any sign that the presence of early stages influenced the performance (that is, mortality or growth) of subsequent predator stages (see Supplementary Information). So in a sense, our individual stages acted like 'independent' predator species, but this may be different for other systems. Further studies are needed to determine whether this pattern is general across systems and taxa.

The stage-structure of natural populations is by no means constant; instead, it frequently changes over time and space with changes in environmental conditions[25,26,31,32]. Furthermore, human activities often do not affect all life stages equally, but instead tend to target specific life stages of natural populations (for example, size-selective harvesting in fisheries[33,34], increased susceptibility to pollutants and pesticides of early stages[35]). Our results indicate that such stage-specific changes or effects have the potential to dramatically alter the functional role of species and ecosystem functioning, or they may have only minor consequences depending on which stage is influenced. Overall, these results emphasize the need for a more holistic view that accounts for the entire life cycle of a species, rather than simply dismissing early or small stages as unimportant for ecosystem function when studying and predicting the ecological roles of species, ensuring ecosystem functioning and managing natural ecosystems.

Methods

Focal species. We used larvae of the salamander *A. talpoideum* as a focal species. This species is widespread throughout the coastal plain of the southeast USA. It typically has one main breeding event per year in our study region in the late winter–early spring after heavy rainfalls. Because reproduction is highly synchronized among individuals, different stages typically do not coexist, as individuals leave ponds after metamorphosis and adults are terrestrial and leave ponds after reproduction. Field observations[36] and experiments[37–39] indicate that ambystomatid salamander larvae are important predators that heavily influence community structure in fishless ponds (reviewed in ref. 40). Salamander larvae are restricted in the size of prey they consume by the size of their mouths[41,42]. As a consequence, the behaviour, diet and micro-habitat use of larval salamanders changes over their ontogeny with changes in body size[43,44]. Early and intermediate stages in our experiment could consume small invertebrates and early tadpole stages, but not larger invertebrates (such as large pulmonate snails, adult backswimmers) or late/large tadpole stages, while the final salamander stages were not gape-limited and could consume all invertebrate and vertebrate species. Furthermore, early predator stages were vulnerable to predation by predatory invertebrates (such as predatory backswimmers, beetles and dragonfly larvae). For the experiment, we obtained eggs of *A. talpoideum* from one fishless pond in the Davy Crockett National Forest, Texas, on 6 March 2010.

Experimental design. To identify the relative impact and functional role of developmental stages and their interactive effects on community structure and ecosystem processes, we used 2 × 2 × 2 factorial design that manipulated the presence or absence of successive ontogenetic stages of *A. talpoideum* in experimental ponds at three different times during their development (ontogeny) (Fig. 1). These treatments resulted in eight types of community that differed in their history with respect to the succession of ontogenetic stages of the apex predator. Each of the three ontogenetic periods (early, intermediate, late) was more than 4 weeks (i.e. 30–31 days) long and together they covered almost the entire larval period of *A. talpoideum*. The last period was 1 day longer due to weather conditions that prevented sampling the experiment. For treatments where individuals were added at intermediate or late stages, individuals in the respective stage were obtained by grouping individuals within a block from all mesocosms based on size and then randomly assigning to treatments within a block. This mixing procedure assured that predator treatments differed only in the presence or absence of salamander stages but not in the environment that salamanders experienced previously (that is, to prevent carry-over effects). Salamander density started at 90 (0.09 ind. l^{-1} or 34.6 ind. m^{-2}; dry mass: 15.6 mg ind.$^{-1}$) and was reduced by 75% after each cohort period to 20 (0.02 ind. l^{-1} or 7.7 ind. m^{-2}, 34.2 mg ind.$^{-1}$) and 5 (0.005 ind. l^{-1} or 1.9 ind. m^{-2}, 78.8 mg ind.$^{-1}$) for the intermediate and late stage to mimic natural mortality and avoid unnatural high densities at larger, older stages. All three densities are within the range of natural densities for the given stage we recorded using box sampling (range = 0–120 ind. m^{-2}, mean = 44.8 ind. m^{-2}). Each treatment was replicated six times except for early (E) + intermediate (I) + late (L), which was replicated twice per block (twelve times) because it served as 'stock' mesocosms to assure that we had enough salamanders for the next ontogenetic stage in case of high mortalities. This created a total of 54 experimental ponds arranged in a complete, randomized block design. The experiment started when salamanders were grouped by size and individuals within a size class were randomly assigned to mesocosms on 8 March 2011 and ended after 3 months on 9 July 2011.

Experimental communities. The experiment was carried out in mesocosms that closely mimicked the structure and complexity of local, semi-permanent, fishless ponds that are naturally inhabited by *A. talpoideum*. Following general procedures of previous protocols[7,12], mesocosms were established in 1,200 l plastic stock tanks set up in a randomized complete block design at Rice University's South Campus Experimental Facility, Houston, Texas. All mesocosms were filled with 1,000 l of de-chlorinated tap water on 23 March 2009. On 27 March, we added 19 l of dried leaf litter mixture (~95% oak lives, 5% pine straw) collected from the margins of two local fishless ponds. All mesocosms were covered with 50% shade cloth lids, which provided natural shading levels. The lids allowed a variety of small to medium-sized invertebrates to colonize the mesocosms while keeping larger predators (except larvae of the dragonfly *P. flavescens*) out and metamorphs (insects and amphibians) in. The mesocosm community consisted of 'permanent' species, which complete their entire life cycle in the mesocosm and went through multiple generations during the three months of our experiment, and 'transient' species, which complete only part of their life cycle in ponds. To establish the permanent species, we added 1 l of concentrated zooplankton (herbivores consuming phytoplankton and zooplankton predators) on 27 March, 500 ml of a highly concentrated mix of amphipods and isopods (herbivores and detritivores) on 10 and 14 April, 20 *Buenoa scimitra* and six adult *Notonecta indica* (pelagic predators) on 11 April and four large pulmonate snails (*Helisoma*

trivolvis) (herbivores consuming periphyton) on 26 April to each mesocosm. All animals were collected from two local salamander ponds. In addition to these permanent inhabitants, the offspring of many species (for example, amphibians, many aquatic insects) only temporarily inhabit natural ponds at different points during the course of the season. These 'transient' species are a major food source for salamanders and important drivers of ecosystem processes. Thus, to recreate the seasonal change in community composition in our mesocosms, we visited local ponds at regular intervals (or whenever major rain events that might initiate amphibian reproduction occurred), collected newly laid clutches of amphibians (and *Epitheca semiaquea* dragonflies) and added the hatchlings to the mesocosms. To each mesocosm, we added 20 recently hatched *P. triseriata* tadpoles on 21 April, 66 grey tree frog (*H. versicolor*) hatchlings on 26 April, 90 hatchlings of the gulf coast toad *Bufo (Incilius) nebulifer* on 10 May, 60 hatchlings of *B. nebulifer* and 60 hatchlings of the bronze frog *Rana (Lithobates) clamitans* on 22 May, and 25 hatchlings of *H. versicolor,* 50 hatchlings of *B. nebulifer* and 100 hatchlings of *R. clamitans* on 18 June, resulting in the total addition (summed across mesocosms and species) of 25,218 tadpoles. In addition, on 19 May we added 25 newly hatched larvae of the dragonfly *E. semiaquea*. All densities are within the lower- to mid-range of natural densities of the respective species. Difference in arrival time among species in our mesocosms directly reflects the natural differences in phenologies of the species during that time period. Together with species that naturally colonized our tanks over the 3 month period (such as various species of chironomid, beetle and mayfly), this created a highly diverse (with >57 morphospecies, and 41 macro-invertebrate, 12 zooplankton and 4 tadpole species) and dynamic community with a natural seasonal turnover in species composition and demographic structure within species. The experiment was terminated on 9 July 2010, just before the largest salamanders reached metamorphosis.

Ecosystem functions and properties. *Decomposition.* We quantified decomposition rates within a mesocosm from leaf litter bags over the entire duration of the experiment. On 3 May 2010, each pond received three leaf litter bags (15 × 20 mm; mesh size: 3.5 mm^2), each filled with 4,000 mg of oven-dried leaves (48 h at 60 °C) from the same random mixture of leaf litter (mostly oak leaves) added to the ponds. We calculated decomposition rates (k) from the exponential decomposition decay curve model with $M_t = M_0 \exp(-kt)$, where M_0 indicates the initial mass of leaf litter bags, M_t the average final leaf litter mass and t is duration of the experiment.

Ecosystem productivity and respiration. Starting on 1 May, we took weekly measurements to estimate NPP and respiration (R) calculated from diurnal oxygen cycles[12,45]. Dissolved oxygen (DO) was measured with an oxygen probe (YSI, Professional Plus) three times a day: at sunrise (t_0), sunset (t_1) and the following sunrise (t_2). NPP is given by the increase in $DO_{t_1-t_0}$, and R by the decrease in $DO_{t_1-t_2}$.

Primary producer biomass. We estimated standing biomass of two dominant forms of primary producer in our ponds, periphyton (benthic algae) and phytoplankton (pelagic algae). Standing biomass of periphyton was estimated weekly from three glass microscope slides per tank (0.74 × 0.25 cm) that were floated separately in the tank for 7 days. After 7 days, glass slides were removed for processing and replaced with a set of new slides. We combined periphyton from both sides of all three slides from the respective sample period for the analysis. Biomass of phytoplankton was quantified from 250 ml water samples collected at mid-water level weekly from each tank. Periphyton and phytoplankton concentrations were then determined fluorometrically (AquaFluor, Turner Designs) through chlorophyll *a* extraction in methanol following standard protocols[46]. We started to collect phytoplankton on 19 April and periphyton on 30 April.

Community structure. We quantified the structure of zooplankton, amphibian and macro-invertebrate (benthic, vegetation and total) communities by counting, measuring and weighing >257,522 individuals from >57 species.

Sampling. We monitored tanks daily for emerging insects and amphibians during the experiment. Amphibian metamorphs were weighed after tail absorption and released at the origin of capture. We converted metamorph wet mass into dry mass using our previously established, species-specific wet to dry mass conversion relationships for amphibians, and a subset of emerged invertebrates was used to calculate species-specific averages for dry mass. Starting on 25 April, we took (unless it overlapped with subsamples) six weekly zooplankton samples at the corner and centre of each tank (total volume: 2.5 l) using a depth-integrated tube sampler. The samples were filtered through 80 µm Nytex mesh, combined and preserved in 75% ethanol. We then determined zooplankton structure by randomly subsampling the combined sample and counting all individuals of a given species. Analysing the whole sample of a set of samples confirmed that this subsample was not biased and adequately reflected the composition and abundances in the larger sample.

At the end of each of the three ontogenetic periods (Fig. 1), we subsampled each mesocosm and removed all salamanders. Because this sampling procedure was highly time consuming and lasted 3 days, we removed salamanders and sampled ponds in two blocks per day, every time in the same order. We subsampled mesocosms in two ways. First, to assure that we collected organisms from all habitat types, we used two perpendicular sweeps at the top and mid water column (including scraping the sides of the mesocosm) with a rectangular 15 cm net with 0.3 mm mesh size, and two perpendicular sweeps with a large (500 µm Nytex mesh) D-net (30.5 cm wide) at the bottom of the mesocosm (including leaf litter). All macro-invertebrates and vertebrates were identified, counted and returned to the mesocosms, and we preserved all small invertebrates in 75% ethanol for later identification. Then we continued sampling the mesocosms to remove and photograph all salamanders and tadpoles in a given mesocosm. Mesocosms without salamanders went through the same procedures. Finally, after the last subsample at the end of the experiment, we destructively sampled the whole mesocosms and collected all macro-invertebrates (≥ 4 mm long) and amphibians until no individuals were left in the tank (hereafter referred to as 'final samples'). All animals were initially preserved in 75% ethanol and stored at −25 °C until further analysis.

We measured final total macro-invertebrate dry mass and final species-specific tadpole dry mass after drying samples at 60 °C for 48 h. Species-specific invertebrate and amphibian dry masses (including emerged individuals) were calculated by measuring body length and/or head width of individuals using image analysis (Image J) and converting them into dry mass using our own and published[47] length–mass regressions. The obtained invertebrate dry mass estimates were not significantly different from the actual weighed dry mass without treatment bias. Larvae and adults of invertebrate species with complete metamorphosis were analysed separately because of their functional differences (for example, beetle larvae versus adults).

All procedures were in compliance with ethical guidelines for animal use and approved by the Institutional Animal Care and Use Committee (IACUC Protocol no. A09022601).

Statistical analyses. *Focal predator survival.* We first tested whether salamander survival, individual and total dry mass (summed across predators) differed across treatments using generalized linear mixed models (GLMM) with binomial error for survival and normal error for mass, treatment as fixed effect and block as random effect. This was done for salamanders after PII and PIII separately using the lme4 package and car package in R[48].

Community structure. Owing to the differences in their life history and sampling procedures, we analysed community structure separately for amphibians, zooplankton and macro-invertebrates. First, we determined how predator treatments influenced each group at the end of each developmental period, that is, after PI, PII and PIII. This allowed us to test how current and past presence of salamander stages affected ecosystem processes. For instance, if E still has an effect at the end of PII, this indicates a 'biological legacy' effect (also called biological inheritance) because the effect of early stages on the ecosystem persists long after it has been gone. It also allowed us to test how such legacy effects alter the impact of subsequent stages on the ecosystem; a significant interaction among past and current stages indicates that effects of subsequent stages were not independent. These analyses were based on abundance because we could not estimate dry mass without killing animals during the experiment.

To quantify amphibian community structure, we combined the number of metamorphs that emerged during a specific cohort period with the tadpoles left at the end of that same period, except for PI, where no amphibians metamorphosed. Community structure of macro-invertebrates was based on subsamples at the end of each period (see methods above), and zooplankton structure, NPP, respiration, periphyton and phytoplankton were quantified using the sample closest to the end of a treatment period.

Finally, we determined how treatments affected the total production (dry biomass and abundance) of amphibians during the entire experiment, including all metamorphs and tadpoles collected at the end of the experiment. The same procedure was used for macro-invertebrates.

We analysed all data in R using GLMM with predator treatment as fixed effect, and block as random effect. Decomposition rate, NPP and respiration rate were analysed using the package lme4 (procedure lmer) with normal distributed errors. To account for zero inflation and overdispersion, we analysed final amphibian biomass (across all species) using the package glmmadmb with negative binomial distributed errors (negBin1) and corrected for zero-inflation. During PI and PII, we had an unwanted invasion of the highly predatory dragonfly *P. flavescens*. Because salamanders were able to eat early stages of *Pantala*, this led to significant differences in *Pantala* abundance across predator treatments. To account for this variation, we included *Pantala* abundance as a covariate when we detected a significant effect of their presence on a given response variable, which was only the case for final invertebrate dry mass. Community composition was analysed and visualized with the vegan package[49] using the adonis procedure based on Bray–Curtis distances and 9,999 permutations. To account for the significant block effects, permutations were constrained within blocks (strata = block). Rare species (present in less than 5% of the samples) were removed from the analysis and abundances (or biomass) were log-transformed. To visualize community structure, we used the non-metric multidimensional scaling (NMDS) ordination

plot function in the vegan package in R; for simplicity, plots do not account for significant block effects.

Predator–biomass correction. In our experiment we used natural densities of each stage. This is the recommended design when predators differ substantially in size, as it avoids many experimental artefacts that would be caused by using designs that keep either biomass or density constant[37,38]. As a side effect of this enhanced realism, differences in biomass inevetibly occur between stages within predator treatments. To test whether these biomass differences among predator stages were largely driving patterns, we conducted several additional analyses.

Community structure can differ among treatments because of changes in the abundances of species, or because of differences in the relative abundances of species. Thus, if total consumption rates of predators are proportional to predator biomass, this could lead to changes in abundances, but would not alter the relative abundances (that is, composition) of species. To differentiate between both scenarios, we analysed community structure of the three functional groups (amphibian, macro-invertebrates, zooplankton) using both total and relative abundances of species. Overall results were qualitatively highly similar, and we thus only present results for relative abundances, given that this analysis is less likely to be affected by differences in biomass across predator treatments.

To correct for predator biomass differences, we also calculated the per unit biomass effect of predators on variables that differed significantly among treatments after the final period, decomposition, amphibian biomass and macro-invertebrate biomass. Specifically, we first calculated the total predator biomass of a given stage at the beginning of their respective period. We then calculated the biomass-corrected effect of different predator treatments on a given ecosystem response variable (X_B) as $X_B = (X_{JP} - X_C)/B_J$, where X_{JP} indicates the value of a given response variable for pond P in predator stage treatment J, X_C is the respective value in the predator-free control and B_J is the average predator biomass in predator treatment J. Positive values of X_B indicate an increase relative to the control and negative values a decrease. We then conducted a GLMM analysis with predator treatment as fixed factor and block as random factor to test for overall treatment effects, followed by planned contrasts that specifically tested for significant differences between single stage treatments (that is, E, I and L; Table 1), early versus late and intermediate versus late using the package multcomp and function glht in R. Results of the biomass-corrected analyses were qualitatively largely similar to the full analyses of predator effects on the untransformed variable (see Results). We did not correct for potential metabolic differences because we do not know the metabolic demands of different stages of *A. talpoideum*. However, because stages often had qualitatively different (that is, had opposite) effects relative to the control, our results are robust to potential differences in metabolic rates, density, or biomass across stages. Furthermore, interaction effects of stages are not affected by these differences.

The per unit biomass effect of predators on decomposition rates was on average five to nine times stronger in treatments with only early or intermediate stages present than in treatments with only late predator stages (E mean relative to control = −0.0216 mg d^{-1} PBM^{-1}, I = −0.0391 mg d^{-1} PBM^{-1}, L = −0.0042 mg d^{-1} PBM^{-1}, where PBM is predator biomass units), but because of the large variation in the L treatment (because values were above and below control), this difference was not significant (Z-test, all $P > 0.05$). However, per unit biomass effects were significantly stronger for early and intermediate stages compared with late stages for total amphibian biomass (E = −1692.3 g PBM^{-1}, I = −1362.9 g PBM^{-1}, L = 487.3 g PBM^{-1}; Z-test: E versus L: $Z = 3.51$, $P < 0.001$; I versus L: $Z = 2.98$, $P = 0.003$, $N = 48$) and final macro-invertebrate biomass (E = 83.7 g PBM^{-1}, I = −57.6 g PBM^{-1}, L = 350.9 g PBM^{-1}; Z-test: E versus L: $Z = 16.9$, $P < 0.0001$; I versus L: $Z = 26.2$, $P < 0.0001$, $N = 48$).

Focal predator survival and growth. On average, 12.1 salamanders died per tank during PI, but mortality rates did not differ significantly across treatments ($\chi^2 = 5.72$, $P > 0.125$). Very few salamanders of cohort 2 and cohort 3 died (>0.4 and 0.3 salamanders died per tank, respectively), and this was not affected by the presence of previous cohorts. Similarly, per capita biomass of salamander larvae did not differ among predator treatments after PII ($\chi^2 = 0.02$, $P > 0.884$) or PIII ($\chi^2 = 5.64$, $P > 0.130$).

Data availability. The community data that support the findings of this study are available in Dryad Digital Repository with the identifier doi:10.5061/dryad.5bm68.

Received 21 June 2016; accepted 21 November 2016; published 13 January 2017

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Acknowledgements

We thank A. Roman, C. Dibble, M. Braun, E. Matson, J. Ohm and G. Ross for help with field work and sample processing, and C. Dibble, B. Toscano and N. Rasmussen for helpful comments on the manuscripts. This work was supported by NSF DEB-1256860 and NSF DEB-0841686 to V.H.W.R.

Author contributions

V.H.W.R. and B.G.V. conducted the experiment together. V.H.W.R. designed the experiment, analysed the data and wrote manuscript with significant input from B.G.V.

Additional information

Supplementary information is available for this paper.

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How to cite this article: Rudolf, V. H. W. & Van Allen, B. G. Legacy effects of developmental stages determine the functional role of predators. *Nat. Ecol. Evol.* **1,** 0038 (2017).

Competing interests

The authors declare no competing financial interests.