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Cross-ecosystem effects of terrestrial predators link treefrogs, zooplankton, and aquatic primary production

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Abstract. Predators can directly or indirectly shape food webs through a combination of consumptive and non-consumptive effects. Yet, how these effects vary across natural populations and their consequences for adjacent ecosystems remains poorly resolved. We examined links between terrestrial predators and aquatic ecosystems through their effects on a locally abundant amphibian, the red-eyed treefrog (*Agalychnis callidryas*), which has arboreal eggs (heavily predated by snakes and wasps) and aquatic larvae; embryos can escape terrestrial threats by hatching at an earlier age and smaller size. Our multi-site field survey indicates that in natural populations, the relative contributions of these consumptive and non-consumptive effects of predators can be substantial and remarkably similar. However, in mesocosms where we experimentally mimicked these predator effects, changes in the density and initial hatching age of tadpoles carried distinct consequences for aquatic food webs. Density-dependent growth resulted in peak tadpole biomass at intermediate densities (reflecting intermediate predation), and early-hatched tadpoles grew 16% faster and produced 26% more biomass than their late-hatched counterparts. These changes in tadpole growth and size differentially affected zooplankton communities, and the production and stability of phytoplankton. Together, these results illustrate multiple pathways through which predators in one ecosystem can modulate the structure of adjacent food webs.

Key words: aquatic–terrestrial linkages; biomass production; coexistence; food webs; life history plasticity; trait and density-mediated effects; trophic cascade.

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INTRODUCTION

Predators can substantially alter prey populations through a combination of changes to the abundance, behavior, morphology, or life history of their prey (Paine 1969, Carpenter and Kitchell 1993, Estes et al. 2011, Costa and Vonesh 2013*b*). Predator–prey interactions often cascade beyond the prey population to shape ecological communities, particularly when the prey is abundant or shifts habitats during their life cycles (Knight et al. 2005, Orrock et al. 2010, Breviglieri et al. 2017). Such cross-ecosystem linkages represent a pervasive yet understudied component of food webs (Polis et al. 1997, Nakano and Murakami 2001, Breviglieri et al. 2017). Moreover, many of the interactions linking adjacent ecosystems may arise through the non-consumptive effects of predators (i.e., changes in prey behavior, morphology, or life history), which are often of greater magnitude than the direct consumptive effects of predators (Schmitz et al. 2004, Trussell

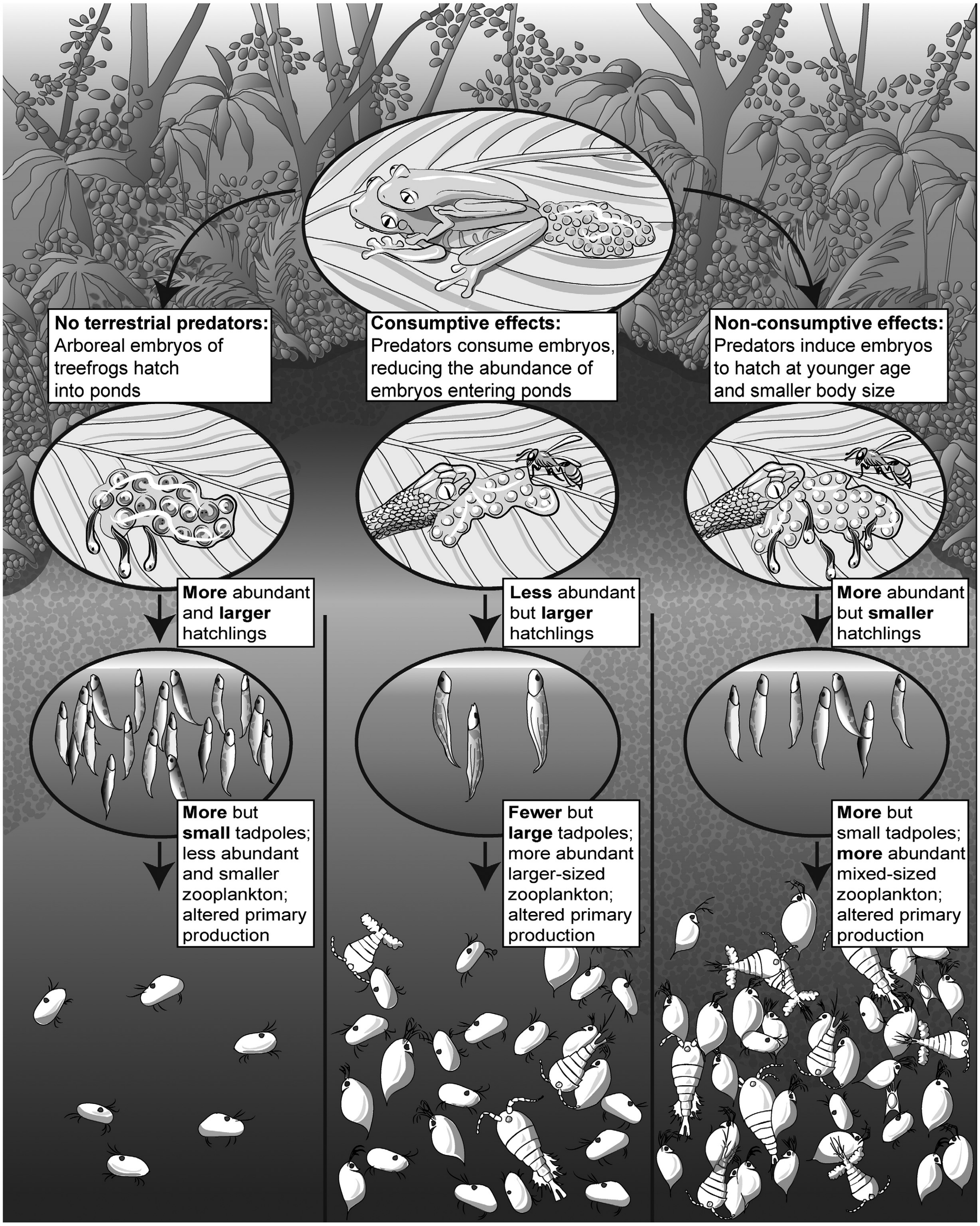

Fig. 1. Hypothesized connections between terrestrial predators, their anuran prey, zooplankton communities, and aquatic primary production. Left vs. central panel: consumptive effects. Snake and wasp predators alter the abundance of tadpole inputs to ponds by consuming arboreal frog eggs. Left vs. right panel: non-consumptive

(Fig. 1. *Continued*)

effects. Predators can also induce tadpoles to hatch early and enter ponds at an earlier age and smaller body size. In both cases, the changes in the density or traits of tadpoles, which are key herbivores in Neotropical ponds, could have cascading effects on tadpole growth and development (e.g., via density-dependent and compensatory growth), zooplankton communities (via competition for algal resources), litter decomposition, and primary production, though the net outcomes of these interactions are difficult to predict a priori. Note, not drawn to scale. Illustration by J. Ferguson.

et al. 2006, Forbes and Hammill 2013, Hammill et al. 2015).

Additionally, several recent studies highlight that the consumptive and non-consumptive effects of predators also differentially alter the body size and overall biomass production of their prey (de Roos et al. 2003, Miller and Rudolf 2011, DeLong et al. 2015, Breviglieri and Romero 2017). For example, predator-driven changes to behavior, morphology, or life history (e.g., hatching time) are often associated with compensatory growth (Warkentin 1999, Doody and Paull 2013), which can shift the size distribution of prey, in turn, altering both intra- and interspecific competition (Gurney et al. 2003, de Roos and Persson 2013). Predators can also indirectly alter the body size of their prey by changing prey abundance, relaxing density-dependent competition and facilitating individual growth and subsequent size-dependent interactions with predators, resources, and competitors (Asquith and Vonesh 2012). Such interactions can substantially affect species composition and ecosystem processes but are typically overlooked in food web studies (Miller and Rudolf 2011, de Roos and Persson 2013).

Here, we examine these interactions using a natural system involving terrestrial predators that alter the abundance and life history of their prey, the red-eyed treefrog (*Agalychnis callidryas*), which switches between terrestrial and aquatic stages. Red-eyed treefrogs are abundant from southern Mexico to northern Colombia and breed throughout the rainy season (generally May–October). Adults deposit their eggs on vegetation overhanging water. Upon hatching, tadpoles drop into the water below where they feed primarily on suspended algae (Savage 2002). During the terrestrial phase, embryos are exposed to numerous threats, including predation by snakes and wasps (Fig. 1; Warkentin 1995, 2000). Predators consume the terrestrial eggs, substantially reducing the abundance of tadpole hatchlings entering ponds (see Fig. 2). However, the arboreal embryos of red-eyed treefrogs respond plastically to these predator threats, often hatching up to 30% earlier than embryos from undisturbed clutches (Warkentin 1995, 2000, 2011*a*); hatchlings from clutches attacked by these predators initially drop into ponds at an earlier age and smaller body size (Warkentin 1995, 1999). Predator-driven changes to both the abundance and traits of tadpoles entering ponds can differentially alter the growth and development of these key herbivores, changing the size and density dependence of competitive interactions between tadpoles and zooplankton, subsequently altering algal resources (Fig. 1).

We examined these aquatic–terrestrial linkages using a field survey and mesocosm experiment. The field survey tracked temporal and spatial variation in predator-driven changes to the abundance and hatching age of tadpoles entering ponds. In the experiment, we mimicked the effects of terrestrial predators by altering either the initial density or age at hatching of tadpoles. We then tracked subsequent effects on aquatic mesocosm communities (with respect to tadpole growth and survival, zooplankton communities, and primary production). We predicted that changes to the initial density or age of tadpoles entering ponds would alter the strength of intraspecific competition and modify tadpole growth. Specifically, we predicted that tadpole biomass would peak at intermediate densities (via density dependence) and that early-hatched tadpoles would grow faster than late-hatched tadpoles (via compensatory growth). In turn, we predicted that these changes would cascade to influence the abundance and composition of zooplankton communities and ecosystem processes such as decomposition and primary production; however, predicting indirect effects such as these remained difficult a priori.

MATERIALS AND METHODS

Consumptive and non-consumptive effects of terrestrial predators: field survey

To quantify the effects of terrestrial predators on the abundance and traits of hatchling inputs to ponds, we conducted a field survey across four breeding ponds near the Smithsonian Tropical Research Institute in Gamboa, Panamá. We sampled ponds throughout the red-eyed treefrog breeding season (June–October). Some ponds were ephemeral; hence, we sampled some ponds for three months, but others up to five months. We used systematic visual encounter surveys to gather two types of data (Donnelly and Guyer 1994, Heyer et al. 2014). First, to quantify the total number of clutches oviposited at each pond (per m^2), we conducted density surveys; every two weeks throughout the breeding season, we counted clutches along randomly placed transects that covered ~25% of the maximum perimeter of each pond. Then, to quantify the consumptive and non-consumptive effects of predators, we also closely monitored a subset of clutches at each pond from the day the clutch was oviposited until all embryos had either hatched or died (days 0–8; following Warkentin 1995, Vonesh 2005).

To estimate the overall attack rate of predators (and any other threats), we counted embryos and monitored them for any signs of damage or mortality. We scored clutches depending on the type and source of damage as either abiotic (flooding, desiccation), predation, undisturbed, or other (e.g., unknown source; eight clutches were attacked by a pathogenic fungus). In addition to missing embryos, all major sources of mortality (e.g., predators, desiccation) leave characteristic signs on the remaining eggs (Warkentin 1995, Vonesh 2005). For example, snakes typically consume large clumps of eggs and leave any remaining eggs undamaged. Wasps, however, remove only one embryo at a time, returning repeatedly to the same clutch, frequently damaging the remaining eggs (e.g., by walking on the clutch). For clutches with multiple sources of mortality, we assigned the clutch to the primary source of mortality (i.e., the largest proportion of eggs killed by that particular source). In this study, our goal was to estimate the effect of predators; therefore, we excluded any clutches with abiotic or other sources of mortality. We fit all statistical models using R (R Development Core Team 2013). To estimate differences in survival between undisturbed clutches and those with predation, we fit generalized linear mixed-effects (GLME) models with binomial errors and the logit link function in the package lme4 (Bates et al. 2012); see Appendix S1 for additional details. We analyzed changes in the density (clutches per m^2) and size (eggs per clutch) of clutches across ponds and sampling periods with GLME analysis (as outlined above) with Poisson errors.

To estimate the effect of terrestrial predators on the recruitment of hatchlings into the ponds (i.e., the consumptive or density-mediated direct effects), we combined data from the density and clutch monitoring surveys and quantified the proportion of hatchlings reduced by predators (embryos killed versus total eggs oviposited; see Appendix S1 for expanded details). Then, using GLME models with binomial errors, we estimated the average predator-driven reductions in the density of tadpoles entering each pond (per m^2) over the course of the breeding season.

We also quantified how predators altered the hatching age of embryos entering ponds (i.e., hatchling tadpoles). Here, we recorded the age (and developmental stage) of the embryos in each new clutch and then tracked each clutch twice daily to record the number and age of eggs/hatchlings until all eggs had either hatched or died (following Warkentin 1995, depending on the time that eggs were oviposited, embryos can turn 5 d old sometime during the age 4 night). We examined the distribution of embryos hatching from day 4 (the age when embryos become hatching competent) through day 8 (beyond which no live embryos remained unhatched). We then quantified whether predator attack altered the proportion of tadpoles per clutch that, on average, hatched early (before day 6; see Fig. 3). Here, we fit a logistic regression model using a generalized linear model (GLM) with binomial errors (Crawley 2007).

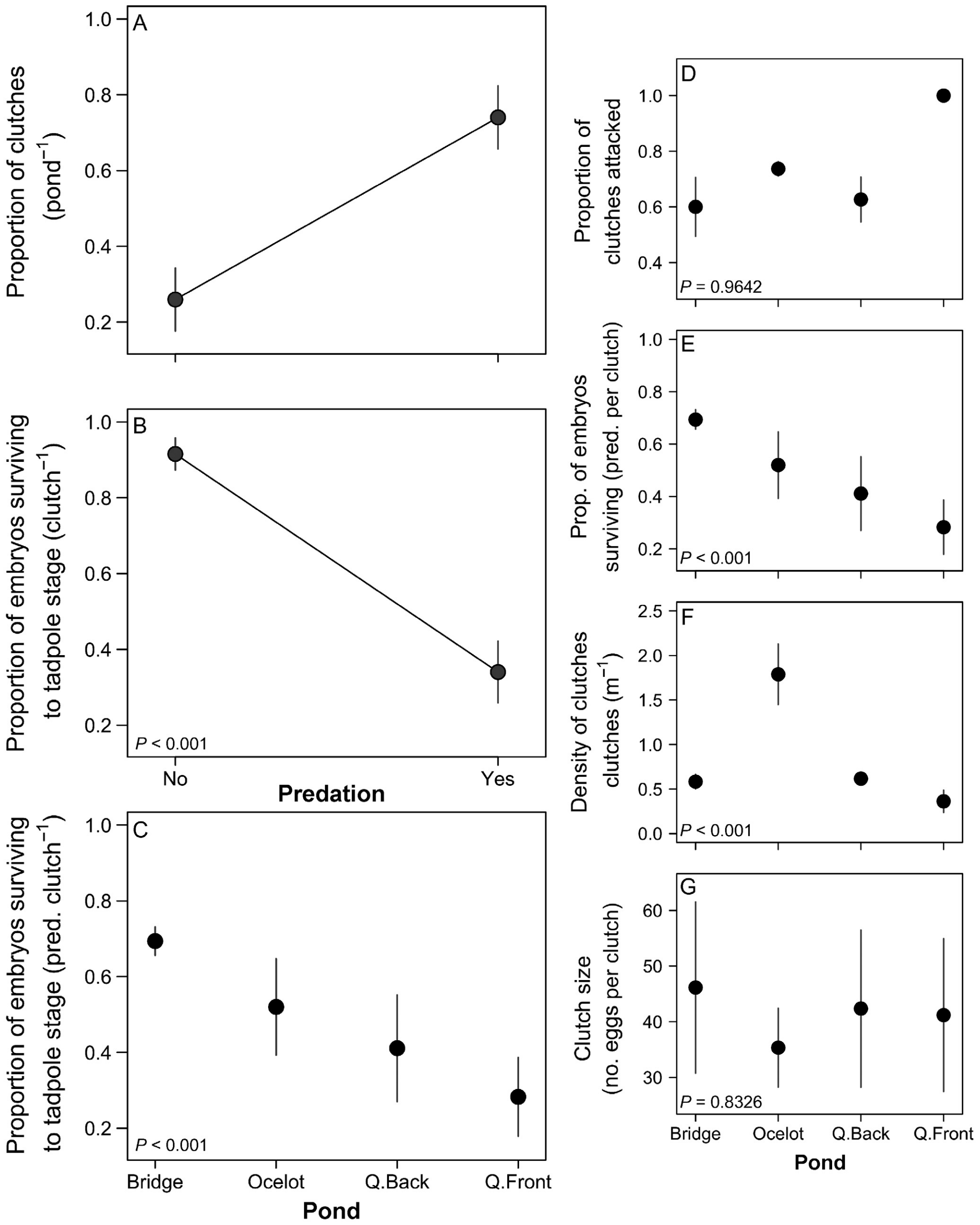

Fig. 2. Consumptive effects of snake and wasp predators on arboreal eggs: field survey. (A) The mean proportion of clutches that were either undisturbed or attacked by terrestrial predators (i.e., excluding clutches with abiotic or other sources of mortality from the analysis). (B) The mean proportion of embryos surviving to the tadpole stage in clutches that were either undisturbed or attacked by terrestrial predators. Each point is the average of the four ponds surveyed throughout the breeding season ± standard error (SE). (C–G) Variation across ponds: (C) the proportion of hatchling inputs reduced by predators (estimated by combining D–G); (D) the proportion of clutches attacked by predators (*P*-value from generalized linear model); (E) from clutches attacked by predators, the proportion of embryos surviving to the tadpole stage; and (F) the average density and (G) size of clutches. Each point is the average of all the clutches surveyed at each pond throughout the breeding season ± SE. Note: Some ponds were ephemeral; we sampled some for three months, others up to five months. *P*-values from generalized linear mixed analysis.

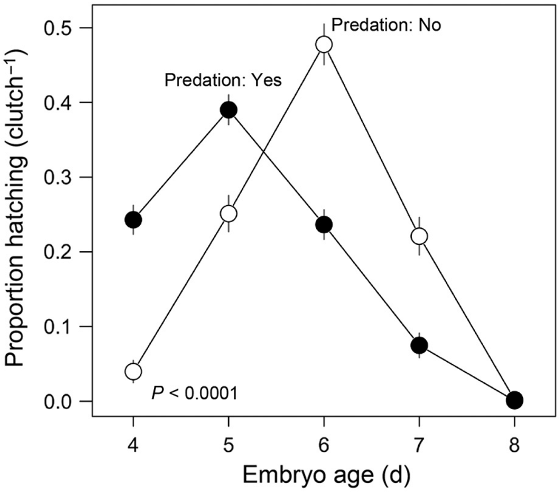

Fig. 3. Non-consumptive effects of snake and wasp predators on arboreal eggs: field survey. Difference in the hatching age (d) of embryos from clutches with and without predation. Each point is the average proportion hatched (±standard error) at each age across all the clutches with predation or without predation. *P*-values are from logistic regressions for proportion data (generalized linear model, GLM).

Consumptive and non-consumptive effects of terrestrial predators: experiment

To understand links between terrestrial predators, their amphibian prey, and aquatic communities, we conducted a mesocosm experiment in which we manipulated either the initial density or the age at hatching of tadpoles (mimicking the effects of terrestrial predators). Obviously, this is a simplified community since tadpoles will also face aquatic predators (Costa and Vonesh 2013*b*). However, our focus here was to quantify trophic interactions between terrestrial predators, tadpoles, zooplankton, and primary producers—all else equal. We used 400-L mesocosms (placed in a shaded field to reflect conditions in the local ponds) stocked with aged tap water, 7 g of rabbit chow, 300 g of rinsed leaf litter (placed inside fine nylon-mesh litter bags), and a 1-L inoculation of concentrated phytoplankton/zooplankton collected from a nearby pond where *Agalychnis callidryas* breed. We covered mesocosms with a mesh top to prevent external colonization and allowed them to incubate for ~2-weeks before adding tadpoles.

Our experiment bracketed the full range of predator-driven changes to tadpole density and hatching age observed in the field survey. To reflect the consumptive effects of predators, we introduced tadpoles over a broad range of densities. Here, our goal was to carefully quantify the (potentially nonlinear) relationships between the initial density of tadpoles and subsequent changes in tadpole growth and aquatic community structure. We introduced tadpoles from undisturbed clutches (i.e., 6-d-old hatchlings with average initial total length [TL] of 11.457 mm) across eight densities (0, 5, 10, 25, 40, 50, 75, and 100), again, reflecting the range of predation pressure we observed in the field survey (see Fig. 2).

To simulate the non-consumptive effects of terrestrial egg predators, we used a density that reflected intermediate levels of predation (40 tadpoles/400 L mesocosm) and compared the effects of age at hatching. To obtain clutches that reflected different developmental stages, we collected freshly oviposited clutches on two mornings 48 h apart (2-d developmental age difference). Late-hatched tadpoles were hatching spontaneously on the day the experiment began, six days after being oviposited (average initial length of 11.46 mm); early-hatched tadpoles (from clutches laid two days later, with average initial length of 9.094 mm) were induced to hatch by gently shaking the clutch. Before releasing tadpoles into the mesocosms, we digitally photographed all tadpoles with a scale reference. Throughout the 6-week experiment, we quantified changes in population, community, and primary production (outlined below). The experiment ended when the first tadpoles metamorphosed.

*Consumptive and non-consumptive effects of terrestrial predators on tadpoles.—*We estimated the effects of predator-driven changes to the initial density and traits of tadpoles. In brief, we measured tadpole survival, growth rates, and total final biomass (see Appendix S1 for methods). We estimated the relationship between initial tadpole density and peak production of total tadpole biomass (per mesocosm) using quadratic regression and the Mitchell-Olds-Shaw test (MOS test; R's vegan package; Mitchell-Olds and Shaw 1987, Mittelbach et al. 2001). For survival data, we fit a logistic regression model using generalized linear analysis (GLM) with binomial errors (Crawley 2007).

*Consumptive and non-consumptive effects of terrestrial predators on aquatic communities.—*To determine how changes in the density and traits of tadpoles affected the pond community and ecosystem properties, each week we sampled zooplankton and primary production (phytoplankton). To quantify effects on aquatic primary production, we collected three separate water samples with an integrated tube sampler. We pooled the water samples, immediately filtered them (pre-combusted, Whatman GF/F, 0.7 μm), extracted the chlorophyll in chilled (4°C) ethanol for 24 h, and then measured algal fluorescence (using a Turner Trilogy Laboratory Fluorometer Sunnyvale, California, USA; Sarnelle and Wilson 2008). We examined differences in the mean and overall stability (using the standard deviation of the mean; Pimm 1984) of primary production.

We identified zooplankton into taxonomic groups at 20×–50× magnification and then calculated total zooplankton density and the percentage of each morphospecies. We examined differences in the density (final and mean) and a proxy for stability of zooplankton communities (i.e., standard deviation of the mean; Pimm 1984) across density and age treatments using correlation analyses and two-tailed *t* tests, respectively. For overall density, we log-transformed data to reduce heteroscedasticity. We also examined whether the community composition of zooplankton varied with initial tadpole density or traits (initial hatching age) using two metrics: (1) distance-based nonparametric multivariate analysis of variance, MANOVA (Anderson 2001), with 4999 permutations (R package npmv; Burchett et al. 2017); and (2) individual correlations (for density) or planned contrasts (for age at hatching treatments). This nonparametric approach addresses problems with multivariate normality, particularly with skewed distributions. Second, we used individual correlations (for density) or planned contrasts (for age at hatching treatments). We asked which, if any, zooplankton taxa differed between treatments, using the relative density of each taxon (i.e., proportion of total zooplankton density). The qualitative relationship between density or hatching-age treatments and zooplankton communities was similar regardless of whether we used total or relative density indices. We also quantified differences in litter decomposition (see Appendix S1 for extended methods).

RESULTS

Consumptive effects of terrestrial predators: field survey

Terrestrial predators significantly altered the density of hatchlings entering the ponds. Overall, we monitored ~6930 eggs from 184 clutches. On average, predators attacked ~74% of all the clutches surveyed (Fig. 2A), and in these clutches, predators reduced the proportion of embryos surviving to the tadpole stage by ~63% (binomial GLME: $\chi^2 = 280.78$, df = 1, $P < 0.001$; Fig. 2B). Terrestrial predators reduced the proportion of hatchlings entering ponds (i.e., hatchling inputs from terrestrial to aquatic environments) by approximately 50%, and these reductions varied considerably across ponds from 21% to 78% (binomial GLME: $\chi^2 = 280.78$, df = 1, $P < 0.001$; Fig. 2C). As outlined above, to estimate these consumptive effects of predators on tadpole inputs into our four focal ponds (averaged over the course of the breeding season), we combined data from the density survey and the field-monitoring survey (Fig. 2D–G): the proportion of clutches attacked by predators, the proportion of embryos surviving to the tadpole stage in those clutches, clutch density, and average clutch size. The proportion of clutches attacked by predators did not differ across breeding ponds (binomial GLM: $\chi^2 = 0.2777$, df = 3, $P = 0.9642$; Fig. 2D). In clutches that were attacked by predators, the proportion of embryos surviving to the tadpole stage differed across ponds (binomial GLME: $\chi^2 = 179.28$, df = 3, $P < 0.001$; Fig. 2E). The density of clutches varied across ponds (Poisson GLME: pond: $\chi^2 = 50.27$, df = 3, $P < 0.001$; Fig. 2F), but the size of clutches (eggs per clutch) was similar across ponds; the average clutch size across all ponds was 38 ± 18 (mean ± standard deviation [SD]: quasi-Poisson GLME: pond: $\chi^2 = 0.8703$, df = 3, $P = 0.8326$; Fig. 2G), and there was no relationship between predator attack and clutch size (predation: $\chi^2 = 1.65$, df = 1, $P = 0.199$).

Non-consumptive effects of terrestrial predators: field survey

Terrestrial predators also altered the hatching age of tadpoles entering the pond (Fig. 3). Averaged across all ponds and over the course of the breeding season, embryos in clutches that were attacked by predators hatched at a younger age

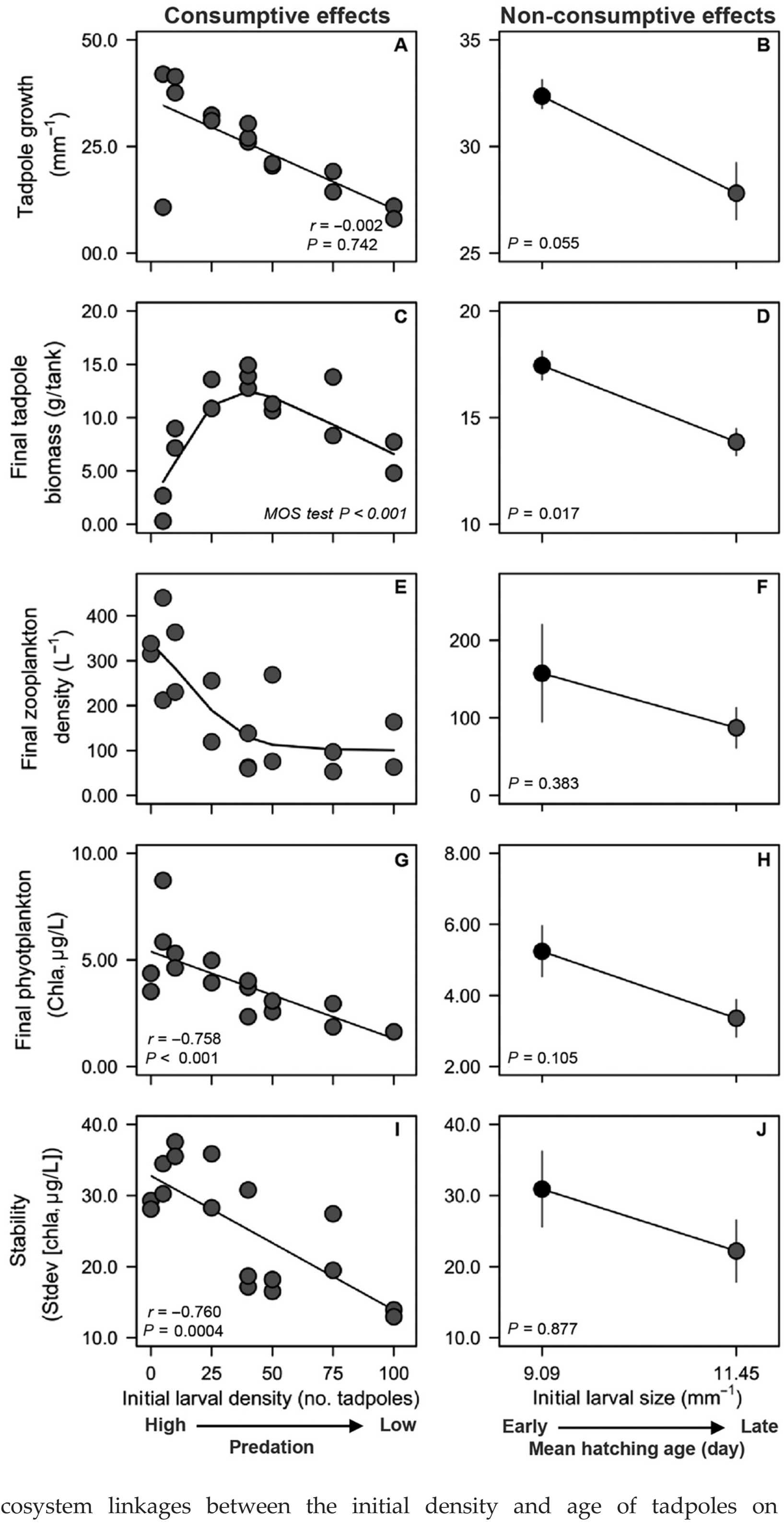

Fig. 4. Cross-ecosystem linkages between the initial density and age of tadpoles on tadpole cohorts,

(Fig. 4. *Continued*)

zooplankton, and primary production. (A–B) Tadpole growth over the 6-week experiment; (C–D) final total biomass of tadpoles; (E–F) density of zooplankton; (G–H) primary production (measured as chlorophyll *a*); and (I–J) stability. For consumptive effects, data points are for individual mesocosms; for non-consumptive effects, data are treatment means ± standard error. Note differences in the axes between the left and right panels.

(GLM: $\chi^2 = 17.10$, df = 1, $P < 0.0001$; Fig. 3). Across all clutches attacked by predators, ~63% of the surviving hatchlings hatched at a younger age (before day 6), relative to hatchlings from undisturbed clutches, from which 70% of hatchlings hatched on or after day 6.

Consumptive and non-consumptive effects of terrestrial predators on tadpoles: experiment

In the mesocosm experiment, the simulated consumptive and non-consumptive effects of terrestrial predators did not strongly alter the overall survival of tadpoles but had distinct effects on tadpole growth and final biomass. Changes in the initial density of tadpoles had no effect on tadpole survival (GLM: $\chi^2 = 0.368$, df = 1, $P = 0.544$; see Appendix S1: Fig. S1A). Overall mortality was also very low in the hatching-age treatments (only 12 of 240 tadpoles died, and seven of these tadpoles were from a single mesocosm). However, there was a slight age-at-hatching effect, in which later-hatched tadpoles had slightly lower survival (GLM: $\chi^2 = 10.19$, df = 1, $P = 0.001$; see Appendix S1: Fig. S1B). Initial tadpole density influenced tadpole growth (Δlength; density effect: Pearson correlation $r = -0.742$, $t = -3.99$, $P = 0.007$; Fig. 4A), whereas initial hatching age had only a marginally significant effect on growth (*t* test; $t = 3.09$, df = 2.96, $P = 0.055$; Fig. 4B). Still, tadpoles that hatched at a younger age (and smaller body size) grew 16% faster than their later-hatched counterparts.

These changes in relative growth rates resulted in pronounced differences in final tadpole biomass. Intermediate reductions in density (mimicking intermediate predation levels from the field survey) increased final biomass by ~12 g (89%) relative to the lowest initial densities and by 8 g (54%) relative to the highest initial densities. There was a significant unimodal relationship between total tadpole biomass and initial tadpole density (Fig. 4C; MOS test, $P < 0.001$) and a significant negative quadratic coefficient (quadratic regression density^2: $P = 0.0002$). In other words, maximum tadpole biomass occurred at intermediate tadpole densities. At these intermediate densities, final biomass of tadpoles that hatched earlier (and at a smaller body size) was 4 g (26%) higher than final biomass of the larger/late-hatched tadpoles (hatching-age effect: $t = 3.94$, df = 3.98, $P = 0.017$; Fig. 4D). Together these results illustrate that both the consumptive and non-consumptive direct effects of terrestrial predators altered the growth trajectories and overall size and biomass distribution of their tadpole prey.

Consumptive and non-consumptive effects of terrestrial predators on aquatic communities: experiment

Changes in tadpole density and initial age at hatching had distinct effects on the density and composition of zooplankton communities. Final zooplankton density was inversely related to final tadpole biomass (density effect: $R^2 = 0.446$, $t = -3.48$, $P = 0.003$; Fig. 4E), and the average density of zooplankton was lower in treatments with higher tadpole densities (Pearson $r = 0.142$, $t = -3.687$, $P = 0.002$). The initial hatching age of tadpoles did not affect the final density of zooplankton (hatch effect: $t = 1.04$, df = 2.66, $P = 0.383$; Fig. 4F) but did affect the average density of zooplankton ($t = 4.82$, df = 3.03, $P = 0.017$). These changes in zooplankton density did not alter the overall stability (SD) of zooplankton communities (density effect: Pearson $r = 0.142$, $t = 0.557$, $P = 0.586$; hatch effect: $t = 0.169$, df = 2.88, $P = 0.877$). We present results on the species composition of zooplankton communities below.

Changes in tadpole density and hatching age altered aquatic primary production and stability (but had no effect on litter decomposition; see Appendix S1). Overall primary production decreased with increasing tadpole density (Pearson $r = -0.635$, $t = -3.19$, $P = 0.006$; Fig. 4G). However, initial age at hatching had no effect on primary production (t = 1.35, df = 3.97, P = 0.247; Fig. 4H). Increasing tadpole density had a stabilizing effect on primary production: Treatments with higher initial densities of tadpoles were significantly more stable (lower SD; Pearson $r = -0.760$, $t = -4.53$, P = 0.0004; Fig. 4I). However, hatch time/initial larval age had no effect on primary production (t = 1.28, df = 3.84, P = 0.877; Fig. 4J). Hence, the trophic cascade arose through the consumptive effects of predators (reductions to the number of tadpoles) rather than their non-consumptive effects (initial changes in the hatching age of tadpoles).

Changes in the community composition of zooplankton were driven largely by changes in the initial age at hatching but not the initial density of tadpoles. Although communities were seeded with zooplankton two weeks prior to the addition of tadpoles and had developed natural variation in zooplankton communities across individual mesocosms, the initial zooplankton communities when we added tadpoles (at week 0) were similar across all treatments (all P-values >0.05). The composition of zooplankton communities did not vary with changes in initial tadpole density (MANOVA: $F_{1,102}$ = 0.808, P = 0.472). Although the overall composition of zooplankton did not change, treatments with higher initial densities of tadpoles had significantly fewer ostracods ($r = -0.609$, $t = -2.97$, P = 0.009; Fig. 5A).

There was, however, a significant effect of initial age at hatching on the composition of zooplankton communities (MANOVA: $F_{1,6}$ = 5.545, P = 0.042). These non-consumptive indirect effects on zooplankton communities were largely driven by differences in herbivorous cladocerans and omnivorous copepods (*Mesocyclops*), which consume both phytoplankton and other zooplankton (Brandl 2005, Sommer and Sommer 2006). With late-hatched tadpoles (where tadpoles grew more slowly), zooplankton communities became dominated by copepods (Fig. 5B, filled bars). However, with early-hatched tadpoles (where tadpoles grew quickly), zooplankton communities had fewer omnivorous copepods (contrast early vs. late hatch; P = 0.0003) and more herbivorous cladocerans (contrast early vs. late hatch; P = 0.0007) but no differences in ostracods (contrast early vs. late hatch; P = 0.0629) or rotifers (contrast early vs. late hatch; P = 0.8612). Thus, the effects of terrestrial predators on the traits, but not the density, of tadpoles significantly altered interspecific competition and shifted the composition of zooplankton communities.

DISCUSSION

Predators can directly or indirectly shape food webs through a combination of consumptive and non-consumptive effects. Yet, the relative

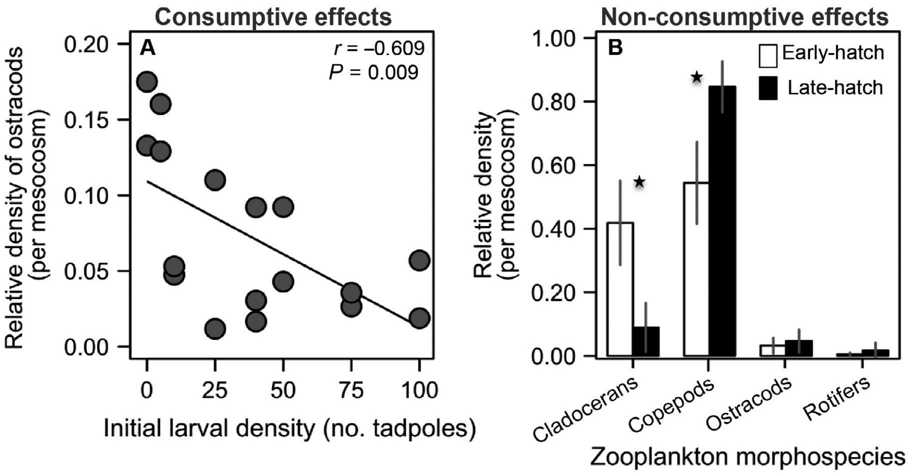

Fig. 5. Links between the initial density and hatching age of tadpoles and the community composition of zooplankton presented as the relative density of each taxon (i.e., proportion of total zooplankton density to account for the variation in density across treatments). Stars indicate significant differences in planned a priori contrasts between hatching treatments. Data represent individual mesocosms (A) or treatment mean ± standard error (B).

contributions of these effects and how they influence natural food webs remain poorly resolved. Our multi-site field survey indicates that the consumptive and non-consumptive effects of predators can be substantial and remarkably similar. Predators attacked ~74.0% of all clutches surveyed, reducing embryo survival to the tadpole stage by ~62.8% and inducing early hatching in ~63.3% of the embryos that survived predator attacks. Similar consumptive effects of predators influence the structure of natural prey populations in birds, frogs, and arthropods (Heske et al. 1999, Hausmann et al. 2005, Vonesh 2005, Mooney et al. 2010). However, while predator-induced shifts in prey life history, including hatching plasticity, are well documented across many systems (Lima and Dill 1990, Benard 2004, Preisser et al. 2005, Warkentin 2011*a*, *b*), few studies have examined how these effects vary across natural populations, over the course of the season (but see Warkentin 1995, Vonesh 2005) or relative to consumptive effects (see Werner and Peacor 2003, Schmitz et al. 2004, Breviglieri and Romero 2017 and references therein).

Our experiment indicates that by changing the density and hatching age of tadpole inputs, terrestrial predators can indirectly alter the structure and functioning of aquatic ecosystems—largely by altering the density and size dependence of competitive interactions among key aquatic herbivores. Our current study cannot elucidate all the mechanisms driving these food web interactions or how the results would change with aquatic predators (Costa and Vonesh 2013*b*). Nonetheless, extensive work on density- and size-dependent interactions in food webs in general (Murdoch et al. 2003, DeLong et al. 2015) and, in particular, amphibians (Wilbur 1997, Asquith and Vonesh 2012) and zooplankton (Hall et al. 1976, Kerfoot and DeAngelis 1989) provides a guide. Again, while some tadpoles consume zooplankton, our previous results suggest that the relationship between red-eyed treefrogs and zooplankton involves competition for resources and not predation; examination of the gut contents and feces revealed no evidence of zooplankton (Costa and Vonesh 2013*a*).

Instead, density-dependent growth regulated tadpole growth and biomass production with subsequent effects on zooplankton communities and primary producers. Small-bodied ostracods (typically 0.3–5.0 mm) became more abundant in mesocosms with fewer tadpoles. In low-density treatments (with a few large but fast-growing tadpoles and abundant small-bodied zooplankton), primary producers became more productive and less stable (i.e., more temporally variable). In agreement with other studies, these patterns suggest that the consumptive effects of terrestrial predators can structure aquatic communities by reducing tadpole inputs which in turn (1) reduce intraspecific competition between tadpoles, (2) facilitate maximal tadpole growth, and (3) allow tadpoles to suppress the abundance of large-bodied zooplankton (cladocerans and copepods) that might otherwise impose strong interference competition (Hall et al. 1976, Kerfoot and DeAngelis 1989, Wilbur 1997, Asquith and Vonesh 2012). In other systems, predators that reduce inputs of prey that use different habitats over their life cycle can modulate the composition and functioning of adjacent food webs. Fish, for example, can indirectly enhance pollination rates in terrestrial plants by reducing the abundance of dragonflies that emerge from ponds and prey on pollinators (Knight et al. 2005). Terrestrial predators reduce seabirds and their sea-to-land nutrient subsidies, consequentially altering the composition of terrestrial plant communities (Croll et al. 2005). In many of these systems, however, the potential non-consumptive effects of these predators remain equivocal.

Here, the non-consumptive effects of predators on the hatching age of tadpoles had strong effects on zooplankton diversity and altered coexistence among tadpoles and zooplankton. Early-hatching tadpoles grew larger (and slightly more quickly) than their late-hatched counterparts, suggesting hyperphagia, compensatory growth, and, thus, stronger interspecific competition (e.g., through interference). However, zooplankton communities became more abundant and more diverse relative to communities with late-hatched (larger but slower-growing) tadpoles. Interestingly, despite these more diverse herbivore communities, primary production increased marginally in mesocosms with early-hatched tadpoles.

Similar cascading effects arising from predator-driven changes to key traits of prey influence the structure of other food webs. For instance, spider-mediated changes to grasshopper behavior altered the biomass production and community composition of plants in old fields (Schmitz 2003). In bromeliads, predator-driven changes to the oviposition behavior of insects shape cross-ecosystem food webs (Romero and Srivastava 2010, Breviglieri et al. 2017). Weaver ants alter the behavior of wasps, shifting the composition of wasp communities toward more pollinators, and increasing pollination and seed production in fig trees (Wang et al. 2014). In all three cases, top predators altered basal resources through non-consumptive effects on their prey.

At least two mechanisms could explain why changes in the initial hatching size of tadpoles had distinct consequences for the composition of zooplankton communities. First, physiological conditions determined by hatching age may have shaped the initial competitive interactions between tadpoles and zooplankton. In many species, including amphibians, early-hatched larvae are smaller, in part because they have had less time to convert their yolk stores into tissue (Warkentin 1999, Doody and Paull 2013). Differences in energy stores may influence other traits that modulate competitive ability (e.g., the onset and rate of feeding); early-hatched tadpoles of *Agalychnis callidryas* begin feeding before later-hatching members of the same egg cohort (Warkentin 1999). Second, early-hatched tadpoles exhibited compensatory growth, often linked with hyperphagia (Gurney et al. 2003). Future empirical and theoretical studies that compare differences in feeding rates between early- and late-hatched tadpoles are needed to help clarify these patterns.

Additional differences in, for example, conversion efficiency associated with compensatory growth (Gurney et al. 2003, Kooijman 2010) could further exacerbate the competitive differences observed between early- and late-hatched tadpoles. Future empirical and theoretical studies can help disentangle links between hatching plasticity, prey bioenergetics, and trophic interactions. Such physiological changes could provide mechanistic insight into why the magnitude of non-consumptive effects of predators often equals or exceeds that of consumptive effects (Schmitz et al. 2004, Preisser et al. 2005). Moreover, future studies could examine these interactions with the added biological realism of aquatic predators which can also influence consumer–resource and competitive interactions by altering tadpole growth rates (Costa and Vonesh 2013b). In the meantime, these results join others suggesting that a focus on how predators modify the development, growth, and size distribution of their prey could provide a more general and mechanistic understanding of how predators influence the structure and function of ecosystems (Miller and Rudolf 2011, de Roos and Persson 2013, DeLong et al. 2015).

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