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Benjamin J. Toscano
Trinity College Hartford

Volker Rudolf

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Benjamin J. Toscano[1,2*]

Volker H.W. Rudolf[2]

[1] Department of Biology, Trinity College, Hartford, Connecticut 06106, USA.

[2] BioSciences, Rice University, Houston, Texas 77005, USA.

[*]Corresponding author: benjamin.toscano@trincoll.edu

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Abstract

Theoreticians who first observed alternative stable states in simple ecological models warned of grave implications for unexpected and irreversible collapses of natural systems (i.e., regime shifts). Recent ecosystem-level shifts engendering considerable economic losses have validated this concern, positioning bistability at the vanguard of coupled human-environment systems management. While the perturbations that induce regime shifts are known, the ecological forces that uphold alternative stable states are often unresolved or complex and system-specific. Thus, the search continues for general mechanisms that can produce alternative stable states under realistic conditions. Integrating model predictions with long-term zooplankton community experiments, we show that the core feature of ontogenetic development, food-dependent maturation, enables a single community to reach different configurations within the same constant environment. In one configuration, predators regulate prey to foster coexistence, while in the other, prey counterintuitively exclude their predator via maturation-limiting competition. The concordance of these findings with the unique outcome and underlying mechanism of a general model provides empirical evidence that developmental change, a fundamental property of life, can support bistability of natural systems.

Introduction

Regime shifts, or transitions between alternative stable states, are increasingly common, occur at multiple biological scales (e.g., population, community and ecosystem), and can result in catastrophic losses of services that humans rely upon (Scheffer and Carpenter 2003; Petraitis 2013). However, the causal mechanisms underlying alternative stable states within natural systems often appear highly complex or system-specific when resolved (Scheffer and Carpenter 2003; Scheffer et al. 2003; Fung et al. 2011; Staver et al. 2011), thereby limiting our ability to predict and prevent the collapses of understudied systems. Thus, identification and experimental demonstration of general, transferable mechanisms supporting alternative stable states is a preeminent research priority.

Recent theory suggests that alternative stable states could be driven by a ubiquitous feature of life: developmental (or ontogenetic) change within populations (de Roos and Persson 2002, 2013; de Roos et al. 2003; Miller and Rudolf 2011; Persson and de Roos 2013; Reichstein et al. 2015). Community-level effects of within-population developmental change derive in large part from a simple condition: newborns must grow (i.e., increase in size) before they can reproduce. This necessity for growth before reproduction implies that juveniles and adults regulate different life-history processes that transfer biomass between developmental stages: maturation and reproduction. Both life-history processes require energy to proceed; basic maintenance costs must be met before individuals can grow or reproduce, and the rates of these processes further increase with energy acquired. Such food-dependence of maturation and reproduction establishes juvenile and adult developmental stages as alternative points of population regulation, for example via differential food limitation (Reichstein et al. 2015). In turn, alternative regulatory points allow for complex feedbacks between the population exhibiting developmental change and the broader ecological community, including alternative stable states (de Roos and Persson 2002, 2013; de Roos et al. 2007; Persson et al. 2007; Persson and de Roos 2013; Reichstein et al. 2015).

Here, we test the hypothesis that food dependent maturation promotes a positive feedback loop associated with alternative community configurations. We study a simple 3-species module termed life-history intraguild predation (LHIGP). This module is prevalent in natural communities (Pimm and Rice 1987; Mylius et al. 2001; Hin et al. 2011) and notable for its hypothesized role in regulating large-scale fishery dynamics (Walters and Kitchell 2001; Gårdmark et al. 2015). Predators within LHIGP systems undergo an ontogenetic diet shift whereby juveniles feed on resources before switching to predating consumers as adults (see food web diagrams in figure 1*b*, 1*c*). While predators can exhibit varying degrees of diet shift within LHIGP systems (van de Wolfshaar et al. 2006; Hin et al. 2011), we focus on the common scenario whereby predators undergo a complete diet shift: juveniles feed exclusively on the resource and adults feed exclusively on consumers (Werner and Gilliam 1984). Importantly, juvenile predators share this resource with competitively-dominant consumers and thus LHIGP systems contain both competition (juvenile predators competing with consumers) and predation (adult predators eating consumers).

The long-term dynamics of LHIGP systems hinge upon the balance of predation and competition (Mylius et al. 2001; Hin et al. 2011; Toscano et al. 2017). Theory predicts that complete diet shift LHIGP systems should exhibit alternative stable states in which: (1) adult predators regulate consumer density to limit competition and foster their own persistence (i.e., a predation stabilizing mechanism); or (2) competitively-dominant consumers reduce resource density to limit juvenile predator recruitment and exclude predators from the system (i.e., a competition stabilizing mechanism) (Hin et al. 2011). While LHIGP has received some theoretical attention (Pimm and Rice 1987; Mylius et al. 2001; van de Wolfshaar et al. 2006; Abrams 2011; Hin et al. 2011), no study has pinpointed the precise factor(s) responsible for supporting alternative stable states in complete diet shift systems. Furthermore, while observational and short-term experimental data are consistent with general LHIGP predictions (Persson et al. 2007; Gårdmark et al. 2015; Toscano et al. 2016), multigenerational experimental tests are lacking, but crucial to establishing the potential for these interactions to support bistability of natural systems.

Our work here combines theory and experiments to explore the potential for developmental change to support different, potentially stable community configurations. We first use theory to demonstrate that food-dependent maturation is the key developmental process that elicits alternative stable states within complete diet shift LHIGP systems; no other potential model, including one with stage-structure alone, predicts that predators cannot invade when rare (i.e., the consumer-resource, competition-dominated state). We then use predator invasion experiments with zooplankton to induce the model-predicted community configurations and show that these configurations persist for multiple generations. We provide further evidence for the positive feedback loop involving stage-specific predation and competition that could stabilize and maintain these configurations over longer time periods.

Methods

Modelling the effects of developmental change on community dynamics

To understand the role of food-dependent life-history processes in driving alternative stable states within complete diet shift LHIGP, we compared 3 predator-consumer-resource models that vary along a gradient of predator developmental change. The first model is a traditional tri-trophic chain with an unstructured predator (figure 1*a*). This model, serving as a "development-free" control, represents the simplest tri-trophic module and has provided the theoretical foundation for top-down regulation (Oksanen et al. 1981). The second features a stage-structured predator that exhibits a complete ontogenetic diet shift (i.e., LHIGP), yet maturation occurs at fixed, food-independent rate (figure 1*b*). The last model differs from the previous only in that maturation is food-dependent (Hin et al. 2011; Toscano et al. 2017) (figure 1*c*). Thus, while all 3 models feature food-dependent reproduction (as most classical ecological models do), only the most developmentally complex LHIGP model incorporates food-dependent maturation.

The basic structure of these models has been previously described (Oksanen et al. 1981; Hin et al. 2011; de Roos and Persson 2013) and thus we present them fully, including our modifications and analysis, in the electronic supplementary material (section S1). In addition to these 3 models (figure 1), we present an unstructured intraguild predation model (Mylius et al. 2001; Hin et al. 2011) serving as an alternative "development-free" control (electronic supplementary material, section S1). All models assumed semi-chemostat resource dynamics. Thus, to produce qualitative predictions, we applied the same generic parameterization to all models and evaluated them along a gradient in resource productivity. We emphasize that our modelling goal was to provide clear, testable, qualitative predictions regarding the effects of developmental change on community structure, rather than to capture the precise dynamics of our empirical system.

Zooplankton experimental system

We used a zooplankton lab system to test for model-predicted community configurations and their associated stabilizing mechanisms. This system (depicted in figure 1*b*, 1*c*) satisfies the basic assumptions of complete diet shift LHIGP. Our experimental predator, the cyclopoid copepod *Mesocyclops edax* undergoes a diet shift in which herbivorous juvenile copepods (i.e., the naupliar or larval stage) feed on the flagellated green alga *Chlamydomonas reinhardtii* before transitioning to carnivory after metamorphosis (Wyngaard and Chinnappa 1982). After metamorphosis, adult copepods feed on other zooplankton (Wyngaard and Chinnappa 1982; Williamson 1984; Adrian and Frost 1993) such as *Daphnia pulex*, the experimental consumer. Juvenile copepods, which differ dramatically in morphology from adults (depicted in figure 1*b*, 1*c*), are specialized filter-feeders and thus cannot feed on zooplankton such as *Daphnia*. There is further evidence that carnivory and thus the ontogenetic diet shift in *Mesocyclops* is obligate: adults fed a pure algae diet (either *Chlamydomonas* or *Cryptomonas ozoli*) fail to produce more than a single clutch of eggs (Adrian and Frost 1993), potentially due incomplete assimilation (Adrian 1987). This is supported by work in our lab which shows that adult *Mesocyclops* cannot reproduce when offered *Chlamydomonas* alone (unpublished data).

In contrast, *Daphnia* undergo no such diet shift and instead function as an unstructured consumer feeding on the shared resource. *Daphnia* are substantially larger than larval copepods, even as neonates, and size-scaling of zooplankton algae clearance rates alone makes *Daphnia* superior to nauplii in algae resource competition (a key-component of the size-efficiency hypothesis: (Hall et al. 1976)). As such, competitive dominance of *Daphnia* over smaller zooplankton, including juvenile *Mesocyclops*, has been well-documented in experimental studies

(Brooks and Dodson 1965; Neill 1975; Romanovsky and Feniova 1985; Vanni 1986; Toscano et al. 2016). In particular, previous work in the same experimental system (Toscano et al. 2016) shows that *Daphnia*, when at high density, are capable of precluding *Mesocyclops* nauplii maturation and survival through depletion of a shared *Chlamydomonas* algae resource. This study, conducted in 250 mL beakers, tracked nauplii from hatching to the young adult stage over a 6-day time period while manipulating *Daphnia* density (Toscano et al. 2016). Thus, the long-term, multigenerational effects of this interaction on zooplankton community dynamics are unknown. The short generation times of these zooplankton (*Mesocyclops* = 1 month in our experimental system, *Daphnia* = 5-10 days) and small size makes them ideal for multigenerational, community-level studies.

Alternative community configurations

We used invasion experiments to test for the model-predicted community configurations, coexistence (predator-presence) and the consumer-resource (predator-absent) state. The complete diet shift LHIGP model with food-dependent maturation (figure 1*c*) predicts that these alternative community configurations can be reached depending on the invading density of predators into the consumer-resource state. Specifically, predators should persist when introduced above their coexistence equilibrium density (leading to coexistence) but succumb to competitive exclusion below this equilibrium density (reverting the system back to the consumer-resource state) (Hin et al. 2011). The complete diet shift LHIGP model with food-dependent maturation is the only relevant model that predicts such qualitative dynamics (figure 1 and electronic supplementary material, figure S1; see also *Discussion*), and specifically the inability of predators to invade when rare. Accordingly, we tested these predictions by adding ovigerous adult copepods (20-40 eggs each; to ensure the presence of juveniles) at different densities to *Daphnia* consumer-*Chlamydomonas* resource communities and tracking dynamics over multiple generations.

We conducted 2 invasion experiments. We first provide methods shared across these 2 invasion experiments and then describe methods specific to each experiment (*Primary invasion experiment*, *Supplemental invasion experiment*). The primary invasion experiment tested for alternative community configurations, while the supplemental invasion experiment was used solely to detect competition and competitive exclusion as a potential driver of predator extinction. While previous work shows that *Daphnia* can preclude *Mesocyclops* nauplii maturation and even survival via competition (Toscano et al. 2016), this supplemental invasion experiment allowed us to explore whether any signals of this interaction exist within community dynamics measured over multiple generations.

Experimental setup

We ran invasion experiments in a semi-chemostat system. The important feature of this system is the use of peristaltic pumps to deliver algae continuously to microcosms housing zooplankton communities. Each cylindrical microcosm (3 L volume) featured four 63 μ nylon mesh-covered outflow holes at the water surface to retain zooplankton but allow suspended particulate matter pass through. This flow-through setup creates semi-chemostat resource dynamics, an assumption of all models. An extended description of the experimental setup including zooplankton collection, medium preparation and algae culture is presented in the electronic supplementary material (section S2). We note here that despite sterilization of the experimental medium, we could not prevent bacterial growth during our experiments. Therefore, it is possible that bacteria served as a secondary, albeit minor resource for filter-feeding juvenile copepods and *Daphnia*.

Microcosms were arranged in adjacent spatial blocks in both experiments. Microcosms within each spatial block shared the same peristaltic pump, algae stock tank and drainage system. Copepod invasion treatments were always interspersed (rather than assigned randomly) within each spatial block. Specifically, we sorted microcosms by their *Daphnia* density at the most recent sampling date and interspersed invasion treatments among the different *Daphnia* densities to ensure that no single treatment was assigned to particularly high or low *Daphnia*-density microcosms.

Primary invasion experiment

The primary invasion experiment (June 2017-October 2017) was designed to induce model-predicted community configurations in the freshwater zooplankton system. We applied 3 treatments, a low invasion density treatment (5 ovigerous copepods added microcosm^{-1}), a high invasion density treatment (100 ovigerous copepods added microcosm^{-1}), and a predator-free control, to 16 consumer-resource microcosms arranged in 2 adjacent spatial blocks. Low and high copepod invasion density treatments were replicated 3 times within each spatial block (6 replicates total per treatment), while the control was replicated twice within each block (4 replicates total). Algae resource density in stock tanks that supplied microcosms was held constant (157,480 cells ml^{-1} in stock tanks) throughout the 4-month duration of the experiment. Microcosms were sampled weekly throughout the experiment (see *Zooplankton sampling*).

Daphnia within the 2nd spatial block crashed independently of predator presence (i.e., in all treatments, including the predator-free control) and thus *Daphnia* were at low density during the copepod predator invasion. While we are unsure of what drove this *Daphnia* crash, its occurrence across the entire experimental block, which was fed from a single algae stock tank, suggests that stock tank contamination could be the culprit. Regardless, in line with theory (Hin et al. 2011), this crash allowed copepods to establish whether they were introduced at low or high density (electronic supplementary material, figure S3) due to reduced competition with *Daphnia*. Accordingly, we present data from the 2 spatial blocks separately.

Supplemental invasion experiment

The supplemental invasion experiment (conducted July 2016-February 2017) was an initial attempt to induce model-predicted community configurations in the zooplankton system. We applied 2 treatments, a low invasion density treatment (20 ovigerous copepods added microcosm^{-1}) and a high invasion density treatment (60 ovigerous copepods added microcosm^{-1}), to 10 microcosms in which the consumer-resource community had been established (5 replicates per treatment). Two separate but identical predator additions were conducted on 7/27/2016 and 9/12/2017. We sampled microcosms once every 4 days in the first few months of the experiment and sampled microcosms once every 2 weeks towards the end of the experiment to check for predator persistence.

In this experiment, zooplankton communities reached the model-predicted community configurations (persisting for up to ~7 copepod generations and ~21 *Daphnia* generations), but invasion density failed to predict final community configurations (electronic supplementary material, figure S4). One potential reason for this was that the intermediate invasion densities used (20 vs. 60 ovigerous copepods microcosm^{-1}, different from those used in the *Primary invasion experiment*) were close enough to the predator equilibrium density whereby environmental stochasticity (e.g., due to variable algae resource density unique to this experiment: electronic supplementary material, figure S4C) or demographic stochasticity could push communities into either feedback loop regardless of their invasion density (Schröder et al. 2005). Indeed, random divergence to different states in identically treated experimental units should be common in systems with multiple attractors (Schröder et al. 2005), and this supplemental invasion experiment could be interpreted as such. Our primary use of this data set, however, was a post-hoc analysis examining the role of competition in driving predator extinction (see *Competitive exclusion*), which occurred in 6 out of 10 microcosms (electronic supplementary material, figure S4b).

Zooplankton sampling

To sample *Daphnia*, we stirred microcosm contents and removed a 200 mL sample from each using a 50 mL Hensen Stempel zooplankton sampling pipette. The first 30 (or less) *Daphnia* individuals within each sample were measured under a dissecting microscope fitted with an ocular. All *Daphnia* within each 200 mL sample were counted. Within the same 200 mL sample, a 150 mL subsample was taken in which juvenile copepods and young adult copepods (i.e., copepodites) were counted. We sampled adult (i.e., reproductive size) copepods using a separate and larger (550 mL) sample volume due to their relatively lower densities. Adults were counted within each 550 mL sample and their reproductive status was recorded. All zooplankton were returned to microcosms after data collection. Zooplankton biomass derivations are presented in the electronic supplementary material (section S3).

Microcosm communities were ended early if we failed to sample copepods, regardless of developmental stage, for at least 3 consecutive sampling events (i.e., at least 3 weeks).

Microcosms in which predator populations declined to zero were considered “predator extinction” communities, while microcosms in which predator populations persisted until the end of experiments were considered “predator persistence” communities.

Testing for the mechanisms stabilizing alternative communities

The LHIGP model with food-dependent maturation (figure 1*c*) posits that coexistence (i.e., the predator-present equilibrium) is maintained by adult predator top-down regulation of competitively-dominant consumers which allows juvenile predators to mature and sustain the adult stage (Hin et al. 2011; Toscano et al. 2016). In contrast, this model posits that the consumer-resource (i.e., predator-absent) equilibrium is driven by competition targeting juvenile predators that limits juvenile maturation, reducing top-down control until predators are excluded (Toscano et al. 2016). We performed analyses on invasion experiment data and conducted an additional juvenile predator rearing experiment to explore these interactions over multiple generations.

Top-down control supporting coexistence

To test the role of adult-driven top-down control in facilitating predator persistence, we compared *Daphnia* biomass density across predator invasion treatments in the primary invasion experiment. We hypothesized that *Daphnia* biomass density would be suppressed to the greatest degree at high copepod invasion density. Such a predation effect would release juvenile predators from competitive regulation to facilitate predator persistence (a positive feedback loop). For reasons described in *Primary invasion experiment*, we tested for top-down control using data from the 1st experimental block.

We tested treatment effects on *Daphnia* biomass density using linear mixed models fit with maximum likelihood (lme4 package (Bates et al. 2014) in the statistical software R). To account for repeated sampling of microcosms, we included microcosm as a random effect in all models. We first tested for treatment effects using post-predator addition data with sampling date included as an additional fixed effect. To test for the maintenance of top-down control throughout the experiment, we excluded data from the low invasion density treatment replicates (ended early due to predator extinction) and tested for an interaction between treatment (high predator invasion density vs. the predator-free control) and sampling date. Significance testing was performed using likelihood ratio tests (lmerTest R package (Kuznetsova et al. 2018)).

Competition leading to predator exclusion

To pinpoint stage-specific competition as the driving force behind the consumer-resource configuration, we used a two-pronged approach. First, to explore the potential for consumers to regulate predators via recruitment limitation, we conducted a juvenile copepod rearing experiment that tested for food-dependent maturation within the same experimental setup used in invasion experiments. This experiment was designed to mimic the effects of resource depletion by *Daphnia* consumers on juvenile copepod survival and maturation. Second, we tested competition as the driver of predator extinction using community time-series data from the supplemental invasion experiment.

While the food-dependence of juvenile maturation has been demonstrated for a number of cyclopoid copepod species (Santer and van den Bosch 1994; Hansen and Santer 1995; Hopp and Maier 2005), we tested this in *Mesocyclops*, the experimental predator. We tested for food-dependent maturation by rearing juvenile copepods across a gradient in algae cell density (i.e., resource productivity). This rearing experiment was conducted within the same semi-chemostat system used for invasion experiments (see *Experimental setup*). We isolated recently hatched juvenile copepods from field-collected adults and divided them evenly into 16 microcosms. We then assigned 3 different *Chlamydomonas* cell density treatments (low-density treatment = 39,319 cells mL^{1}; medium-density treatment = 77,477 cells mL^{1}; and high-density treatment = 150,339 cells mL^{1}) and a no algae control to microcosms with 2 replicates each. Thus, algae cell density within the high-density treatment was roughly equivalent to the algae cell density used in the primary invasion experiment (157,480 cells ml^{-1}). Accordingly, in the invasion experiments, this high-density algae treatment could be considered the resource density if *Daphnia* were absent, while lower cell density treatments in the rearing experiment served as a proxy for the effects of algae resource depletion by *Daphnia*. We sampled microcosms 5 times over the course of 21 days, counting juvenile and young adult copepods within 150 mL samples to track survival and maturation. Extended methods for this experiment are presented in the electronic supplementary material (section S4).

To test the effects of algae cell density treatment on juvenile copepod survival and maturation, we used generalized linear mixed models (lme4 package in the statistical software R) with Poisson error distributions and log links to model count data (survival: total number of copepods sample^{-1}, maturation: number of young adult copepods sample^{-1}). Separate models were constructed for survival and maturation data. In each model, treatment and sampling date were modelled as fixed factors and an interaction between these factors was included to test whether treatments diverged over the 21-day experimental duration with microcosm modelled as a random effect. Our approach to significance testing was to build nested models with and without the factor of interest and compare models using likelihood ratio tests.

To support stage-specific competition as the driving force behind the consumer-resource configuration (see also Toscano et al. 2016), we conducted a post-hoc analysis of community dynamics from the supplemental invasion experiment. We hypothesized that microcosm communities in which copepod predators went extinct would exhibit a clear signal of competition between *Daphnia* consumers and juvenile copepod predators. Identifying a significant competitive effect in communities in which copepods went extinct, but not in communities in which copepods persisted would support competitive exclusion of the predator by its prey.

We used multivariate autoregressive state-space modelling (MARSS, using the MARSS package in R (Holmes et al. 2014)) to test competition as a driver of zooplankton community configurations. MARSS is a linear approximation for nonlinear stochastic multispecies processes that has been used extensively in elucidating interactions among freshwater zooplankton life-stages and species (Hampton et al. 2013). We modelled 3 state processes: *Daphnia* (the competitively-dominant consumer), juvenile copepod predators and adult copepod predators and included density-dependence within each. All potential interactions were set to zero except for those hypothesized to drive community dynamics: the effect of *Daphnia* on juvenile copepods (i.e., competition) and the effect of adult copepods on *Daphnia* (i.e., predation). MARSS incorporates a lag of 1 time-step and thus implicitly excludes interactions that would occur over longer time scales (e.g., a positive effect of *Daphnia* on juvenile copepods via the adult reproductive response). We additionally included a covariate for algae cell density affecting *Daphnia* density because algae cell densities in stock tanks were variable over the course of this experiment. We assumed that each individual time-series had different observational and process (i.e., demographic or environmental stochasticity) errors. Population densities were logtransformed and Z-scored prior to analysis (Hampton et al. 2013). All model fitting was performed using the Expectation-Maximization (EM) algorithm (Hampton et al. 2013).

We first tested for a difference in strength of competition between tanks in which copepod predators persisted (n = 4) vs. tanks in which copepod predators went extinct (n = 6). Separate MARSS models were fit to community time-series data from individual microcosms (10 model fits in total), and we compared competition coefficient values between the 2 groups using a t-test. To test the significance of this competitive effect for each group, we fit 2 separate MARSS models to combined time-series data from predator extinction and persistence microcosms. We then set competition coefficients to zero (i.e., removing the effect of competition) and compared nested model fits using parametric bootstrapped AIC (AICb; 100 iterations) that corrects for bias due to short time-series.

Results

Modelling the effects of developmental change on community dynamics

With food-independent maturation (figure 1*b*), complete diet shift LHIGP produces dynamics indistinguishable from a traditional unstructured tri-trophic chain (figure 1*a*): both models predict a predator-consumer-resource (i.e., coexistence) state as the sole equilibrium at high resource productivity levels. Adult predators dominate total predator biomass density within this coexistence state and their top-down control of competitively-dominant consumers (i.e., a trophic cascade) frees juvenile predators from consumer control (figure 1*b*). Importantly, predators can always invade from low densities beyond a certain productivity threshold (vertical dashed line:

figure 1*b*) because fixed maturation ensures the completion of the predator life cycle despite consumer competitive-dominance.

Adding food-dependent maturation to complete diet shift LHIGP elicits an alternative stable community state absent from traditional model dynamics (figure 1*c*). Whereas fixed maturation guarantees predator persistence (figure 1*b*), food-dependent predator maturation allows competitively dominant consumers to exclude predators through competition in an alternative consumer-resource equilibrium (figure 1*c*). Thus, only the LHIGP model with food-dependent maturation exhibits bistability: a coexistence equilibrium in which predators persist via top-down regulation of consumers, or a consumer-resource equilibrium in which predators are excluded by their prey via competition targeting juveniles (figure 1*c*). Bistability becomes possible at a threshold in resource productivity (vertical dashed line: figure 1*c*). Predators can persist beyond this threshold when introduced at or above their coexistence equilibrium density but can no longer invade from low densities.

Alternative community configurations

In the primary invasion experiment, copepod predators introduced to consumer-resource communities at high density persisted for up to ~4 copepod generations and ~12 *Daphnia* generations, establishing the model-predicted coexistence configuration (figure 2*a*). In contrast, copepods introduced to consumer-resource communities at low density rapidly declined to extinction (i.e., could not invade when rare), reverting the system back to a consumer-resource configuration (figure 2*b*). Thus, consistent with model predictions, different initial conditions (predator invasion densities) led to alternative community configurations within the same constant environment.

Top-down control supporting coexistence

At high copepod invasion density (the treatment in which coexistence was observed), invading adults drove a precipitous decline in the density of competitively-dominant consumers (likelihood ratio test: $\chi2 = 13.111$, $p < 0.001$) (figure 3*a*), mitigating potential negative effects of competition on the initial juvenile copepod predator cohort. This cohort successfully recruited to the adult stage (figure 2*a*), sustaining top-down regulation (no interaction between treatment and time, likelihood ratio test: $\chi2 = 2.0442$, $p = 0.1528$) (figure 3*a*) and completing the predation-regulated feedback. In contrast, copepods at low invasion densities failed to significantly reduce consumer biomass density ($\chi2 = 0.7623$, $p = 0.3826$) (figure 3*a*) and quickly declined to extinction because the first juvenile predator cohorts (100-200 individuals per tank) never matured (figure 2*b*).

Competition leading to predator exclusion

We found that both juvenile copepod survival (treatment effect, likelihood ratio test: $\chi^2 = 49.734$, $p < 0.001$) and maturation ($\chi^2 = 10.746$, $p = 0.013$) were limited at low algae resource levels (figure 3*b*), thereby establishing food-dependent maturation and the potential for competitive exclusion by competitively dominant *Daphnia* prey.

MARSS applied to long-term data from the supplemental invasion experiment revealed significantly lower (i.e., stronger) competition coefficients in predator extinction vs. predator persistence communities (two-tailed t-test comparing competition coefficients among final community configurations: $t_9 = -4.5715$, $p = 0.002$) (figure 3*c*). Furthermore, competition was a significant driver of community dynamics in predator extinction communities (mean competition coefficient ± standard error: -0.3907 ± 0.1320, comparison of models with and without competition term: ΔAICb = 23.97), but not in predator persistence communities (0.00184 ± 0.1432, ΔAICb = 1.05).

Together, these additional data support a causal chain in which competitively-dominant consumers, left unchecked under weak adult-driven top-down forcing (figure 3*a*), excluded their predator within the low invasion density treatment group, i.e., predators could not invade when rare in the primary invasion experiment (figure 2*b*).

Discussion

Natural systems often undergo large, abrupt, and persistent transitions in structure and functioning (Scheffer and Carpenter 2003; Petraitis 2013), yet identifying general biological mechanisms underlying alternative stable states has proved challenging. Many studies on alternative stable states rely purely on observation, are unreplicated, or are not closely matched with theory (Schröder et al. 2005; Petraitis 2013). Our study provides two forms of evidence suggested to conclusively demonstrate alternative stable states (Schröder et al. 2005): (1) we manipulated initial conditions to show that our model zooplankton community can reach both hypothesized configurations within the same environment; and (2) results of our supplemental invasion experiment indicate random divergence to different community configurations in identically-treated experimental units. Schröder et al. (2005) further suggests that at least one complete system turnover is necessary to demonstrate alternative stable states (see also (Connell and Sousa 1983; Sousa and Connell 1985)), and our experiments spanned up to 7 predator generations and 21 consumer generations. Last, we use theory to rule out alternative explanations for experimental dynamics, and provide evidence for the stage-specific interactions, predation and competition, that could stabilize and maintain these community configurations over longer time periods (see also (Toscano et al. 2016)). Taken together, these findings suggest a central role for food-dependent maturation, a fundamental aspect of ontogenetic development (de Roos and Persson 2013), in supporting alternative community configurations within our empirical system.

Alternative community configurations: Correspondence between theory and data

By manipulating the invading density of predators, we induced coexistence (predator-present) and consumer-resource (predator-absent) community configurations within the same constant environment. These community configurations could only be predicted by the LHIGP model with food-dependent maturation – all other plausible three-species model variants, which contained food-dependent reproduction only (including an unstructured intraguild predation model: electronic supplementary material, figure S1), failed to predict these particular dynamics. Instead, these models predicted that predators could always invade when rare, and thus coexistence as the sole community state. This included a model with stage structure and an ontogenetic diet shift, suggesting these features are not sufficient to substantially alter dynamics from the unstructured model. Finally, a LHIGP model containing realistic developmental change in which adult predators broaden their diet (i.e., feeding on both the consumer and the resource, rather than undergoing a complete shift to consumer consumption), predicts predator-resource and consumer-resource alternative stable states (van de Wolfshaar et al. 2006; Toscano et al. 2017), and thus cannot explain community dynamics within our experiments.

Traditional models lacking developmental change are increasingly criticized because they represent a unique scenario in which food-dependent life-history processes occur implicitly in perfect symmetry, yielding a single homogeneous population structure (de Roos and Persson 2013). The conditions for such symmetry are likely rare in nature. Instead, food-dependence of maturation and reproduction allows for differences in the rates of these life-history processes and thus asymmetries in the biomass densities of different developmental stages as observed within natural populations (de Roos and Persson 2013). Accordingly, as we demonstrate here, food-dependent life-history processes can lead to a wider range of potential dynamics than predicted by traditional models, including alternative stable states (Miller and Rudolf 2011; de Roos and Persson 2013; Persson and de Roos 2013). Indeed, recent work incorporating developmental change into other community modules has effectively overturned long-standing predictions from fundamental theory (de Roos and Persson 2013), helping to explain incongruence between unstructured model predictions and complex natural dynamics.

Positive feedback loops: Stage-specific species interactions

Positive feedback loops are commonly associated with alternative stable states (Scheffer and Carpenter 2003; Petraitis 2013; Kéfi et al. 2016) and recent theory suggest that such feedback loops are likely to arise in systems with food dependent life-history traits and stage-specific species interactions (van de Wolfshaar et al. 2006; Hin et al. 2011; de Roos and Persson 2013; Toscano et al. 2017). The LHIGP model with food-dependent maturation tested here predicts that predators can foster their own persistence by predating consumers that compete with juvenile predators (Hin et al. 2011; Toscano et al. 2017). While previous empirical work demonstrated this positive feedback loop at a smaller scale spatial and temporal scale (Toscano et al. 2016), the present study shows that it also influences zooplankton community structure over multiple generations. We found that the predator-present state (coexistence) was associated with top-down control of consumers by adult predators, while the predator-absent state was associated with a lack of top-down control and the complete absence of juvenile predator recruitment. Specifically, in each of three low predator-density invasion treatment replicates, 100-200 recently hatched juvenile predators failed to mature despite high algae resource densities in our semi-chemostat system. While our study did not measure algae resource levels and thus cannot distinguish between exploitative and interference mechanisms (MacIsaac and Gilbert 1991), the evidence presented here and elsewhere (Toscano et al. 2016) is consistent with role of competition in driving juvenile copepod recruitment failure in our experimental system, both via reduced rate of maturation and ultimately death. For example, in our food-dependent maturation experiment run at the same algae resource level, we show that juvenile copepods have plenty of food to mature in the absence of *Daphnia* competition, but experimentally reducing algae resource levels, as we expect *Daphnia* to do, leads to almost complete recruitment failure. While this positive feedback loop is specific to LHIGP systems, we argue that given the prevalence of food-dependent maturation and stage-specific indirect interactions within natural populations, the ultimate mechanism established by this study could be an important driver of alternative stable states across a wide range of ecological systems.

Notable in our study was the speed of predator exclusion and its likely relation to the competitive dominance of *Daphnia* prey. Competitive dominance of *Daphnia* over smaller zooplankton, such as juvenile *Mesocyclops* copepods, is a core assumption of the size-efficiency hypothesis (Hall et al. 1976) with considerable empirical support (Brooks and Dodson 1965; Neill 1975; Romanovsky and Feniova 1985; Vanni 1986; Toscano et al. 2016). Thus despite the presence of demographic stochasticity in our study among high predator invasion density (i.e., coexistence) treatment replicates, predator exclusion occurred quickly and completely across low invasion density treatment replicates. In contrast, we expect the relative importance of such stochastic processes to increase with competitive symmetry with a slower time to exclusion. While our experimental study provides a relatively long-term demonstration of alternative community configurations (Schröder et al. 2005), it remains unknown whether the predator-present coexistent state could persist indefinitely within our lab system. Perturbation studies that induce predator mortality and test for predator rebound or collapse (i.e., regime shift) would provide a clear experimental test of stability in our experimental system.

Prey excluding predators

Predator regulation by prey (i.e., consumers) via stage-specific competition is opposite to the typically-held view that predators regulate prey through consumption, yet potentially more widespread than previously thought. Classic studies show that by inflicting mortality, predators can drive their prey extinct, as seen in predator invasions of islands (Savidge 1987; Schoener et al. 2001; Blackburn et al. 2004), biological control (Murdoch et al. 1985), and throughout the fossil record (Vermeij 1977; Sallan et al. 2011). Nevertheless, the overwhelming majority of studies treat predator populations as homogenous units and overlook functional differentiation within (Werner and Gilliam 1984; de Roos and Persson 2013). Given that juvenile and adult predator developmental stages often interact horizontally with different species due to ontogenetic diet shifts (Werner and Gilliam 1984; Miller and Rudolf 2011), juvenile predators often face consumers that are competitively superior in resource competition (Werner and Gilliam 1984; Toscano et al. 2016). This makes juvenile predators susceptible to maturation or recruitment limitation and thus stage-structured predator populations uniquely vulnerable to extirpation or extinction (Purvis et al. 2000; Ray et al. 2013). Furthermore, because this vulnerability of predators manifests within an alternative stable state, predators' susceptibility to exclusion may remain hidden within natural communities until a tipping point is crossed. Such has been proposed in Atlantic cod (*Gadus morhua*), where rebound from overfishing has been potentially halted by competition between their juvenile cod and prey (though other explanations exist for these dynamics: Gårdmark et al. 2015). Thus, our controlled zooplankton experiments demonstrate potential mechanisms underlying the dynamics of other systems that are harder to manipulate.

Applications and conclusion

Regime shifts can result in unexpected and catastrophic ecosystem service losses and may increase in frequency due to environmental forcing under global change scenarios or top predator removal from marine and terrestrial ecosystems (Estes et al. 2011). Yet, predicting these shifts has proved challenging because empirical drivers of alternative states often appear complex and system-specific (Fung et al. 2011; Petraitis 2013). The sensitivity of community dynamics to developmental change revealed here and its ubiquity within natural communities suggests that managers should monitor changes in the size or stage structure of populations, in addition to total population or adult densities. Early warning signal detection applied to stage-specific biomasses could prove a useful, though underutilized, strategy for predicting regime shifts if statistical signatures are masked at coarser scales of biological measurement (though these signals may not be universal: (Boerlijst et al. 2013)). While collecting such data for all species would be logistically challenging, we direct focus to lower-order systems with disproportionately strong (i.e., keystone) interactions (Estes and Duggins 1995; McCann et al. 1998) such as the one studied here. New ecological theory incorporating within-population developmental change (de Roos and Persson 2013) could be used in concert to target community modules that are particularly sensitive to changes in population size or stage distributions. Given the ubiquity of developmental change, we expect these strategies to enhance our capacity to predict and manage regime shifts in the future.

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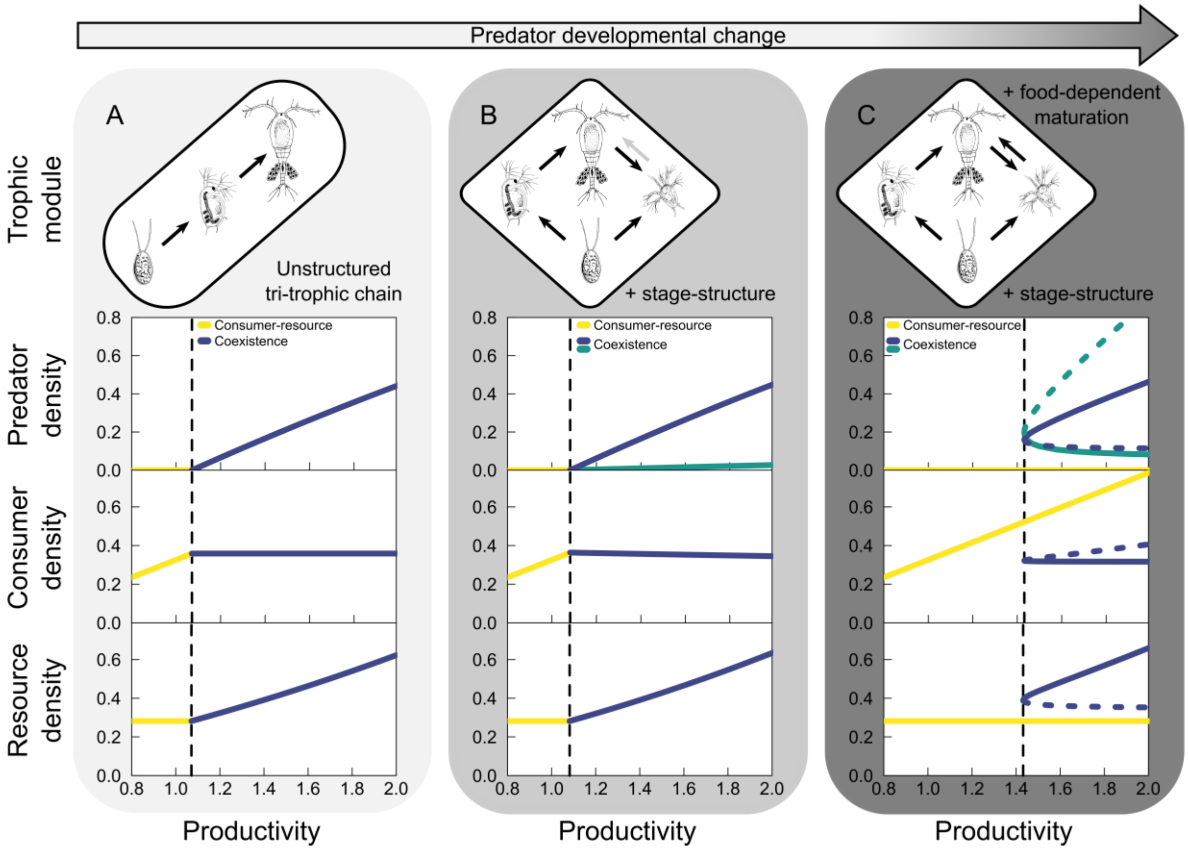

Figure 1. Community-level effects of developmental (ontogenetic) change in predator-consumer-resource trophic modules: model equilibria over a productivity gradient. (A) Traditional tri-trophic chain with an unstructured predator population (i.e., “development-free” control). (B) Stage-structured module with fixed predator maturation. (C) Stage-structured module with food-dependent predator maturation (electronic supplementary material, table S1 for equations). Trophic modules are illustrated with the zooplankton system used to test model predictions. Solid arrows within modules represent food-dependent pathways of energy transfer, while gray arrow in stage-structured module (B) represents fixed (i.e., food-independent) maturation. Model predictions (equilibrium densities over a productivity gradient) are depicted below modules. Solid lines depict stable equilibria and dashed lines depict unstable equilibria. The consumer-resource equilibrium is shown in yellow, while the coexistence (predator-

consumer-resource) equilibrium is shown in blue. In the tri-trophic chain (A), unstructured predator density is indicated with a blue line, while in the stage-structured modules (B, C), juvenile predator density is indicated with green lines and adult predator density with blue lines. Vertical dashed lines mark different productivity thresholds at which a qualitative change in equilibria occurs. In (A) and (B), the vertical dashed line marks the productivity threshold at which predators invade the consumer-resource equilibrium. In (C), the vertical dashed line marks the lowest productivity at which coexistence becomes possible as an alternative stable equilibrium. Parameters shared among models are set to the same values (electronic supplementary material, Table S3).

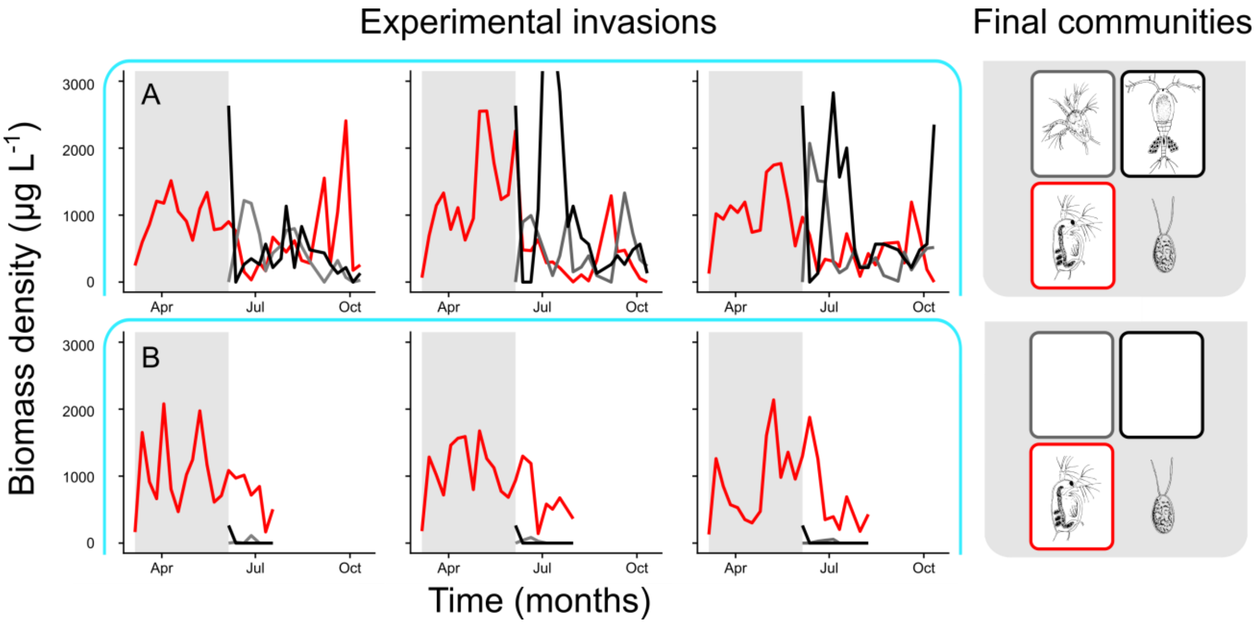

Figure 2. Experimental copepod predator invasions into replicate consumer-resource communities at high (A) and low (B) copepod invasion densities. Each panel depicts the dynamics from a single replicate microcosm within either the high or low invasion density treatment group. Shaded regions of panels mark community dynamics prior to predator invasion. Copepod predators in the high invasion density treatment persisted for ~4 generations while *Daphnia* persisted for ~12 generations. Zooplankton diagrams to the right of invasion panels depict final community configurations for both simulated and experimental invasions, with rectangle colors indicating biomass density lines in invasion panels (*Daphnia*: red; juvenile copepods: grey; adult copepods: black; algae not depicted in invasion panels). No predator controls and additional treatment replicates are shown in electronic supplementary material, figure S2 and figure S3, respectively.

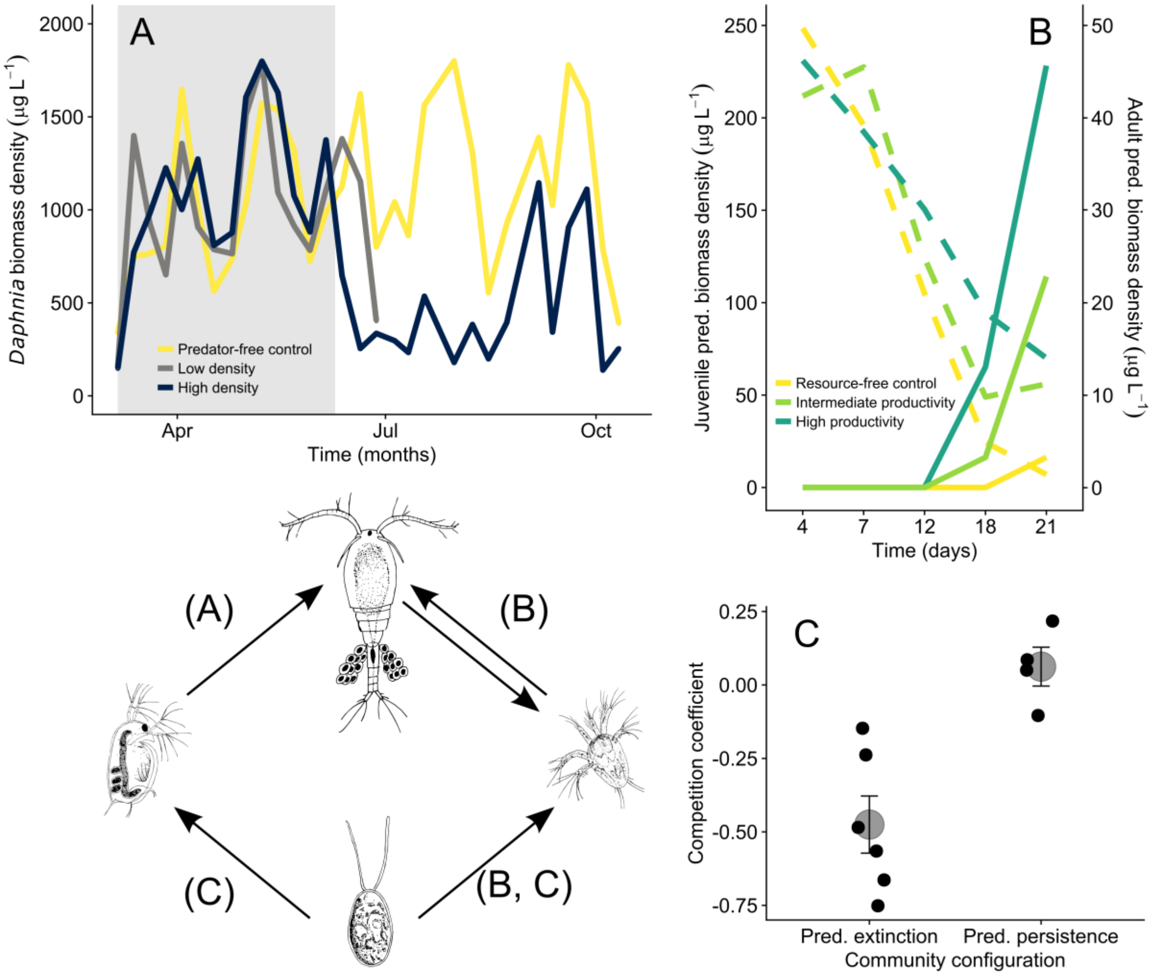

Figure 3. Stage-specific interactions maintaining alternative stable states. (A) Top-down effects of copepods (invasion density treatments) on mean consumer (*Daphnia*) biomass density over the course of the experiment (see figure 2 and electronic supplementary material, figure S4 for microcosm-level dynamics; error bars omitted for clarity). Low density predator invasion treatment microcosms were terminated early due to predator extinction. Shaded region marks community dynamics prior to predator invasion. (B) Effects of resource productivity (algae cell density treatments) on mean juvenile copepod recruitment into the adult stage (low- and medium-productivity treatment replicates were combined for plotting ["intermediate

productivity"]; error bars omitted for clarity). Dashed lines indicate surviving individuals and

terial, figure S4).