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Trophic cascades alter eco-evolutionary dynamics and body size evolution

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Trait evolution in predator–prey systems can feed back to the dynamics of interacting species as well as cascade to impact the dynamics of indirectly linked species (eco-evolutionary trophic cascades; EETCs). A key mediator of trophic cascades is body mass, as it both strongly influences and evolves in response to predator–prey interactions. Here, we use Gillespie eco-evolutionary models to explore EETCs resulting from top predator loss and mediated by body mass evolution. Our four-trophic-level food chain model uses allometric scaling to link body mass to different functions (ecological pleiotropy) and is realistically parameterized from the FORAGE database to mimic the parameter space of a typical freshwater system. To track real-time changes in selective pressures, we also calculated fitness gradients for each trophic level. As predicted, top predator loss generated alternating shifts in abundance across trophic levels, and, depending on the nature and strength in changes to fitness gradients, also altered trajectories of body mass evolution. Although more distantly linked, changes in the abundance of top predators still affected the eco-evolutionary dynamics of the basal producers, in part because of their relatively short generation times. Overall, our results suggest that impacts on top predators can set off transient EETCs with the potential for widespread indirect impacts on food webs.

1. Introduction

Human-induced predator loss has strong effects on prey populations that cascade through non-adjacent trophic levels and lead to changes in ecosystem structure and function [1–10]. Until recently [11], the study of trophic cascades has mostly focused on changes in abundance and ecological functions. Increasing evidence for a feedback between ecological and evolutionary processes in short time scales (eco-evolutionary dynamics [12–14]), however, suggests the possibility that the changes in abundance caused by trophic cascades also would lead to trait evolution in species indirectly linked to the top predators (or eco-evolutionary trophic cascades; EETCs [11]). Yet we know little about the selective forces transmitted to more distantly interacting species and how these changes might influence the strength of a trophic cascade.

EETCs can arise because both traits and abundance drive the strength of interactions between predators and prey [15,16] (electronic supplementary material, appendix S1). Traits that govern the functional response, for example, influence the strength of predation and lead to changes in predator and prey abundance. Changes in traits, then, can lead to changes in abundance, further changes in traits and altered interaction strengths. For example, Wood *et al.* [11] showed that traits linked to a competition–defense trade-off can evolve across trophic levels in response to changes in top predator abundance. Among the many possible traits that could mediate EETCs, body mass is particularly important given its link to the strength of trophic cascades [17,18] and shifts under altered selection regimes [19,20].

Body mass has multiple effects on the functions driving population dynamics and food webs (ecological pleiotropy) [6]. For example, the parameters of the functional response scale with predator and prey body mass

within and across species [21–23]. In addition, predator conversion efficiency depends on both predator and prey body mass because smaller prey yield less energy and larger predators are more costly to produce [24]. Finally, life-history traits are strongly tied to body mass [25–28]. Despite understanding the impact of body mass on a wide array of ecological functions, it is not known how the rapid evolution of body mass across a food chain might alter trophic cascades.

To evaluate body mass-mediated EETCs, we used as a case study an allometric food chain model (e.g. [29]). We simulated the dynamics of all populations in the food chain using Gillespie eco-evolutionary models (GEMs) [24,30,31] that allow the body mass of populations at each trophic level to evolve. We implemented our model with four trophic levels intact and then evaluated the resulting EETC set off by the extinction of the predator in the fourth trophic level. We specifically evaluated the model for evidence that: (i) eco-evolutionary dynamics throughout the food chain will respond to the loss of the top predator; (ii) eco-evolutionary dynamics will alter trophic cascade magnitude; and finally, (iii) because trophic cascades initiated by the loss of top predators are by definition in a transient state [32] and impacts might take time to propagate across trophic levels, there would be a lag in detectability of the EETC in more distantly interacting species.

2. Material and methods

(a) Food chain model

We used a modified MacArthur–Rosenzweig (MR) ordinary differential equation (ODE) model for changes in the abundance of phytoplankton (P), zooplankton (Z), zooplanktivorous fish (F) and piscivorous fish (W) [33]. We used logistic growth for the basal resource (phytoplankton) with the intrinsic rate of population growth r and carrying capacity K . A type II functional response connects the levels with predation. The functional response has two parameters: space clearance rate (a subscripted by the predator) and handling time (h subscripted by the predator). We also include resource-dependent mortality, where mortality rates reach a maximum (d subscripted by that species) when no prey is present and increasing prey levels reduce mortality rates [34]. This function uses a Michaelis–Menton curve with a half-saturation constant indicated by the prey type subscripted with a K . Finally, predators convert ingested prey into new consumers with a conversion efficiency (e subscripted by the predator). For parameter definitions, mean starting values and typical starting ranges see electronic supplementary material, table S2:

$$\frac{dW}{dt} = \frac{e_W a_W F W}{(1 + a_W h_W F)} - \left(d_W - \frac{d_W F}{F + F_K} \right) W, \quad (2.1a)$$

$$\frac{dF}{dt} = \frac{e_F a_F Z F}{(1 + a_F h_F Z)} - \frac{a_W F W}{(1 + a_W h_W F)} - \left(d_F - \frac{d_F Z}{Z + Z_K} \right) F, \quad (2.1b)$$

$$\frac{dZ}{dt} = \frac{e_Z a_Z P Z}{(1 + a_Z h_Z P)} - \frac{a_F Z F}{(1 + a_F h_F Z)} - \left(d_Z - \frac{d_Z P}{P + P_K} \right) Z \quad (2.1c)$$

$$\text{and } \frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - \frac{a_Z P Z}{(1 + a_Z h_Z P)}. \quad (2.1d)$$

(b) Model parameterization

We parameterized equations (2.1a–d) with realistic values to approximate a freshwater lake food chain (electronic supplementary material, table S2). We used the FoRAGE database [35] to

identify representative functional responses for the foraging of zooplankton on phytoplankton [36], zooplanktivorous fish on zooplankton [37] and piscivorous fish on zooplanktivorous fish [38]. Because functional responses across taxa are frequently type II [39], we implemented our model with this form. With these values, upper trophic level interactions drove prey extinct, so we reduced the space clearance rates of these functional responses until the system persisted over several months. This reduction is consistent with the idea that laboratory-based estimates of functional responses are steeper than they might be in real systems, since prey behaviour, spatial heterogeneity, physical structures, turbidity or alternative prey consumption can reduce functional responses in natural settings [40]. Mean initial space clearance rates (functional response parameter a) used were 4.55, 42 and 27 300 cm³ per predator per day for zooplankton, zooplanktivorous fish and piscivorous fish, respectively. Handling times, kept at their estimated values from the FoRAGE database, were 1.5×10^{-6} , 2×10^{-4} and 1.36×10^{-2} days for zooplankton, zooplanktivorous fish and piscivorous fish, respectively.

We chose starting body masses at the lowest three trophic levels by averaging masses of organisms that would occupy such levels in an aquatic system from the FoRAGE database [35]. Starting masses were 4.86×10^{-7} , 7.91×10^{-1} , 2.9×10^2 and 2.5×10^4 mg for phytoplankton, zooplankton, zooplanktivorous fish and piscivorous fish, respectively. We chose the body mass of the piscivorous fish as approximately 100× that of the zooplanktivorous fish as that reflects a realistic value for fish predator–prey body mass relationships [41]. We made the food chain model allometric by constructing scaling relationships for the functional response, conversion efficiency and mortality rate parameters (electronic supplementary material, table S2).

We used the scaling equation from McCoy & Gillooly [42] to estimate the maximum death rate for each consumer, where the maximum death rate (day^{−1}) $d = d_0 M^D$, d_0 is the death rate when $M = 1$, and D is a scaling exponent. Without empirical estimates of these values, we simply selected half-saturation constants for the mortality functions as ones that helped to stabilize the dynamics. The mass dependence of conversion efficiency e (unitless) was calculated as $e_{TL} = E(M_{TL-1}/M_{TL})$, where E is the gross growth efficiency, M_{TL-1} is the mass of the prey and M_{TL} is the mass of the predator at trophic level TL . We set E to 0.2 (unitless) for all species, which is a mid-range estimate for aquatic consumers [43].

We made the functional response parameters (space clearance rate and handling time) functions of both predator and prey body mass, as is commonly found in many taxa [22,39]. The space clearance rate model was $a = a_0 M_{TL}^{AC} M_{TL-1}^{AR}$, where a_0 is the space clearance rate when $M_{TL} = M_{TL-1} = 1$, M_{TL} is the mass of the consumer (upper trophic level), M_{TL-1} is the mass of the resource (lower trophic level), AC is the scaling exponent on the consumer and AR is the scaling exponent on the resource. Analogously, we made handling time a function of both predator and prey mass: $h = h_0 M_{TL}^{HC} M_{TL-1}^{HR}$, where h_0 is the handling time when $M_{TL} = M_{TL-1} = 1$, HC is the scaling exponent on the consumer and HR is the scaling exponent on the resource. In general, larger prey will take longer to handle and larger predators can handle a given prey in less time, so we set $HC = -0.5$ and $HR = 0.25$ for all trophic interactions. Likewise, larger predators are able to clear space more effectively than smaller predators, so we set $AC = 0.5$. Our results are qualitatively similar across a range of scaling parameters of the same sign.

We chose two prey mass scaling scenarios for the space clearance rate. First, larger prey may be selected less often because they are harder to capture (i.e. AR is negative), hereafter referred to as the negative scaling scenario. Second, larger prey may be selected more often because of their greater energy return or detectability (i.e. AR is positive), hereafter referred to as the positive scaling scenario. Thus, our two scenarios set the scaling of

space clearance rate with prey mass as either $AR = -0.25$ or $AR = 0.25$. We calculated the values of a_0 and h_0 such that space clearance rates were equal to our chosen starting values at the starting body masses of the appropriate species.

(c) Eco-evolutionary dynamics and GEMs

To permit simultaneous ecological and evolutionary dynamics, we simulated equation (2.1) with GEMs. GEMs simulate ODE models by turning rates into discrete events whose probabilities are proportional to the relative magnitude of the rate term (as in a Gillespie simulation) [30]. GEMs differ from standard Gillespie simulations by representing populations with distributions of traits (here body masses) that influence parameters (e.g. a , h , e and d) and thus the likelihood of events, rather than with constant parameters. In our simulations, populations at all trophic levels begin with random draws from a lognormal distribution with the initial target mean and a coefficient of variation (CV) of 0.3.

After initial population creation, GEMs function by choosing an individual at random from the population and calculating model terms based on the individual's trait(s). Events (birth, death, predation) are then chosen at random given their probability. Once the event is selected, an individual (represented by a trait) is added to or removed from the population. In the event of a birth, an 'offspring' trait is added following heritability rules (see details in [31]). Briefly, offspring traits are chosen by random draw from a distribution that is centred on the expected value of the parent's trait and a standard deviation calculated from the equation for a parent-offspring regression. Thus, an offspring trait will look more like its parent when heritability is high and population variation is small. In the event of a death, the current trait is removed from the distribution. The cycle continues through more events until the desired end time is reached. Evolution occurs in these simulations because traits that increase the likelihood of birth get added to the trait distribution more often and traits that lower the likelihood of death are removed from the distribution less frequently. As a result, trait distributions move toward traits that maximize the ratio of expected births to expected deaths (i.e. expected lifetime reproductive success).

For these simulations, we picked a body mass from each population (i.e. one mass for phytoplankton, zooplankton, zooplanktivorous fish and piscivorous fish) and calculated parameters given the scaling equations for each trophic level described above and in electronic supplementary material, table S2. Narrow-sense heritability for body mass in all populations was 0.75. Because the time cost of handling prey occurs after a predation event, not beforehand, we used the population-level averages of predator and prey body mass for the handling time to mimic the expected time cost of prey consumed at the previous time step. We then calculated the rate terms in equation (2.1) from that complete parameter set and used these to determine the probability of events across all four trophic levels.

Although there are several modelling approaches potentially suitable for assessing EETCs [44], GEMs are particularly useful because they easily accommodate simultaneous evolution in multiple populations, track trait distributions (rather than only means) through time, and inherently include the effects of demographic and individual stochasticity and genetic drift on trait evolution. In GEM simulations, eco-evolutionary dynamics arise from the stochastic birth-death process [45] and do not make the assumptions about constant additive genetic variance [46], separation of ecological and evolutionary time scales [47] or large population size [48] generally need for quantitative genetics and adaptive dynamics approaches [46,49]. An alternative approach would be individual-based models [11], but GEMs provide greater computational efficiency and a clear pairing with ODEs such that the fitness gradients can be calculated from the derivative of the per capita growth rate with respect to body mass.

(d) Rescaling the spatial dimensions of each population

In our model, the number of individual phytoplankton required to support populations at the fourth trophic level is very high. Constructing a GEM with phytoplankton populations in the billions put a severe computational burden on our simulations. We, therefore, rescaled the sizes of each population, such that we tracked the populations at lower trophic levels in successively smaller volumes. This is also consistent with the idea that the scale over which zooplankton interact with each other is smaller than that of a highly mobile piscivorous fish. We implemented this rescaling by adjusting the volume dimensions of functional responses (electronic supplementary material, table S3). For example, we tracked the number of phytoplankton in a millilitre and the number of zooplankton in a litre. To rescale the foraging, we adjusted the space clearance rates of zooplankton to millilitre and the abundance of zooplankton to number per millilitre in the phytoplankton equation but adjusted them to litre in the zooplankton equation. This rescaling permitted us to initiate our food chain with smaller populations at each level, specifically 800 phytoplankton in a millilitre, 200 zooplankton in a litre, 200 zooplanktivorous fish in a kilolitre and 200 piscivorous fish in a megalitre, based on realistic density estimates in temperature ponds.

(e) Inducing and assessing eco-evolutionary trophic cascades

We used both standard numerical solvers and GEM simulations of equation (2.1) to generate dynamics. First, we solved the ODE with initial parameters and all four trophic levels intact. This solution is our 'ecology only baseline' scenario. Then, we ran the same ODE but removed all the piscivorous fish at time step 50, starting the ODE solution over again at this point to see the continuing dynamics unfold after the loss of the top predator. This solution is our 'ecology only trophic cascade' scenario.

We then ran GEMs in two complementary scenarios, both with the initial CV in body mass set to 0.3 for all populations. First, we ran our GEM to allow eco-evolutionary dynamics to occur at all trophic levels throughout the food chain. These simulations are our 'eco-evo baseline' observations (all trophic levels intact). Second, we ran the same GEM but removed all the piscivorous fish at time step 50. These simulations are our 'eco-evo trophic cascade' observations. Prior to running GEMs with evolving traits, we set the CV to 0 and ensured that GEMs without evolution largely mirrored ODE solutions.

Our analysis focuses on the transient dynamics of a 400-day period. This length of time is sufficient for eco-evolutionary dynamics to unfold in aquatic interactions such as those between zooplankton and phytoplankton [50,51]. We do not explicitly consider the change in trophic cascades at the equilibrium of our model, because (i) the parameterization we used leads to dynamics that do not reach an equilibrium solution for many years, (ii) analytical expressions for the eco-evolutionary equilibria of this model are highly cumbersome and (iii) we are specifically interested in the transient dynamics of this system given the disequilibrium state set off by the loss of the top predator.

Detecting EETCs depends on being able to distinguish changes in abundance and traits resulting from eco-evolutionary interactions from that of the trophic cascade itself. To do this, we used a bivariate plot of the per cent change in abundance and body mass to visualize the effects of trophic cascades in the absence of body mass evolution (ecology-only trophic cascade) versus the resultant effects of trophic cascades in systems with eco-evolutionary feedbacks (EETC) (figure 1). Furthermore, we plot the relative change in both abundance and body mass at regular time intervals (dotted lines) to illustrate transient changes in abundance and body mass. Ecology-only trophic

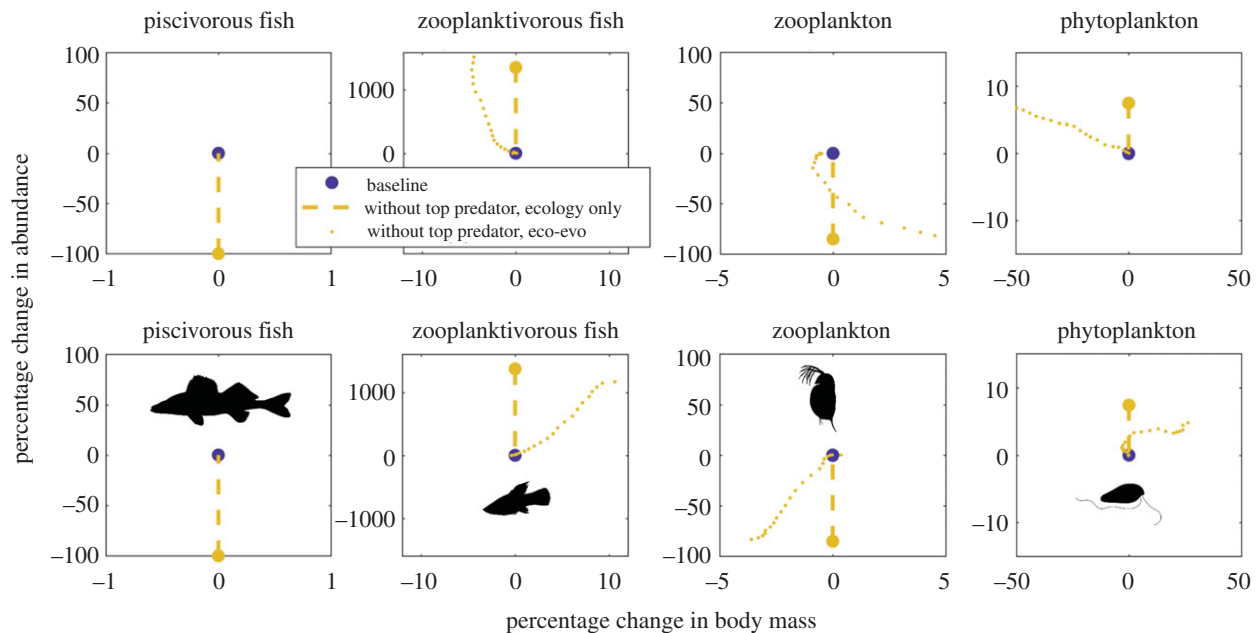


Figure 1. How much a trophic cascade alters the abundance and size of organisms differs when evolution (dotted yellow line) is incorporated. Trophic levels are arranged from apex predator (left) to producer (right). Negative scaling scenario (functional response gets shallower with prey size; top row) and positive scaling scenario (functional response gets steeper with prey size; bottom row) prey scaling scenarios are depicted (see text). Each line depicts the change in body size and abundance from systems without trophic cascades (blue dot) caused by a trophic cascade in the absence (dashed line) or presence (dotted line) of evolution. For the dotted line, dots are shown at regular time intervals to illustrate rates of change in body size and abundance (e.g. increasing distance between dots indicates accelerating change). (Online version in colour.)

cascades emerge as a shift from the all-trophic-levels-intact baseline (blue dot) along the yellow dashes after a trophic cascade induced by removing the top predator. Ecology-only trophic cascades only move the yellow dashes up or down to reflect shifts in abundance. Trophic cascades and eco-evolutionary dynamics could potentially co-occur without affecting each other, however, they must affect each other to create EETCs. Thus, eco-evolutionary dynamics have to change the magnitude of a trophic cascade, and or trait evolution during a trophic cascade has to differ from that of the eco-evolutionary baseline (i.e. trophic cascade changes trait evolution). EETCs will thus manifest in the bivariate plot as deviations from the ecology-only trophic cascade when corrected for background eco-evolutionary dynamics in the absence of trophic cascades. Changes in the rates of how much EETCs diverge from background eco-evolutionary dynamics emerge as increasing (accelerating) or decreasing (decelerating) distances between dots.

To understand how the loss of the top predator causes selective forces to cascade down the food chain, we also calculated the instantaneous fitness gradient for each trophic level across time. We did this by taking the derivative of the per capita growth rate of each population with respect to that species's body mass. These functions are complicated due to the fact that body mass is present in multiple power-law terms in the model. Nevertheless, each fitness gradient contains terms that capture the effects of body mass on births and deaths due to predation and natural mortality. In this way, shifts in species abundances alter the magnitude of the terms and change the fitness gradients. We calculated the fitness gradient with the abundances, trait values and parameters of the median GEM outcomes through time.

3. Results

Trophic cascades resulting from the simulated loss of the piscivorous fish were clearly visible in both ecology-only (ODE, dashed lines) and eco-evo (GEM, solid lines) models with

alternating increases and decreases in abundance from zooplanktivorous fish through to phytoplankton (figure 1). In agreement with recent empirical studies [16], the effects of rapid evolution on trophic cascade-induced changes in abundance were largely cryptic (y -axis, figure 1). However, trophic cascades clearly altered eco-evolutionary dynamics (deviation from dashed lines; figure 1) indicating feedbacks between the loss of a top predator and the eco-evolutionary dynamics of an unperturbed system.

The direction and magnitude of relative changes in body mass varied with trophic level and scaling scenario (figures 2 and 3, middle column). When trophic cascades reduced predator populations of zooplanktivorous fish and phytoplankton, they evolved relatively smaller masses in negative scaling simulations and larger masses in positive scaling scenarios (figure 1). In both scenarios, this difference was caused by trophic cascades dampening body mass evolution (figures 2 and 3, centre column) through reduction in selective pressure (fitness gradient generally moves towards 0, EETC figures 2 and 3, right column). Trophic cascades increased predation pressure on zooplankton and their body mass evolved in directions consistent with increased predation pressure (e.g. smaller under positive scaling). However, the relative overall magnitude of zooplankton mass evolution was the smallest of the three trophic levels potentially due to being between trophic levels exerting opposing selection forces.

Solutions to our models were highly dynamic, such that the trophic cascade tended to increase through time after predator removal (figures 2 and 3, left column). The transient nature of the EETCs in the GEM simulations was readily apparent (e.g. figure 1, zooplankton top row), with continual shifts in abundance and traits through time across trophic levels and scaling scenarios (figures 1–3). Furthermore, variation in body mass evolution trajectories among simulations (figures 2 and 3, centre column) was generally amplified

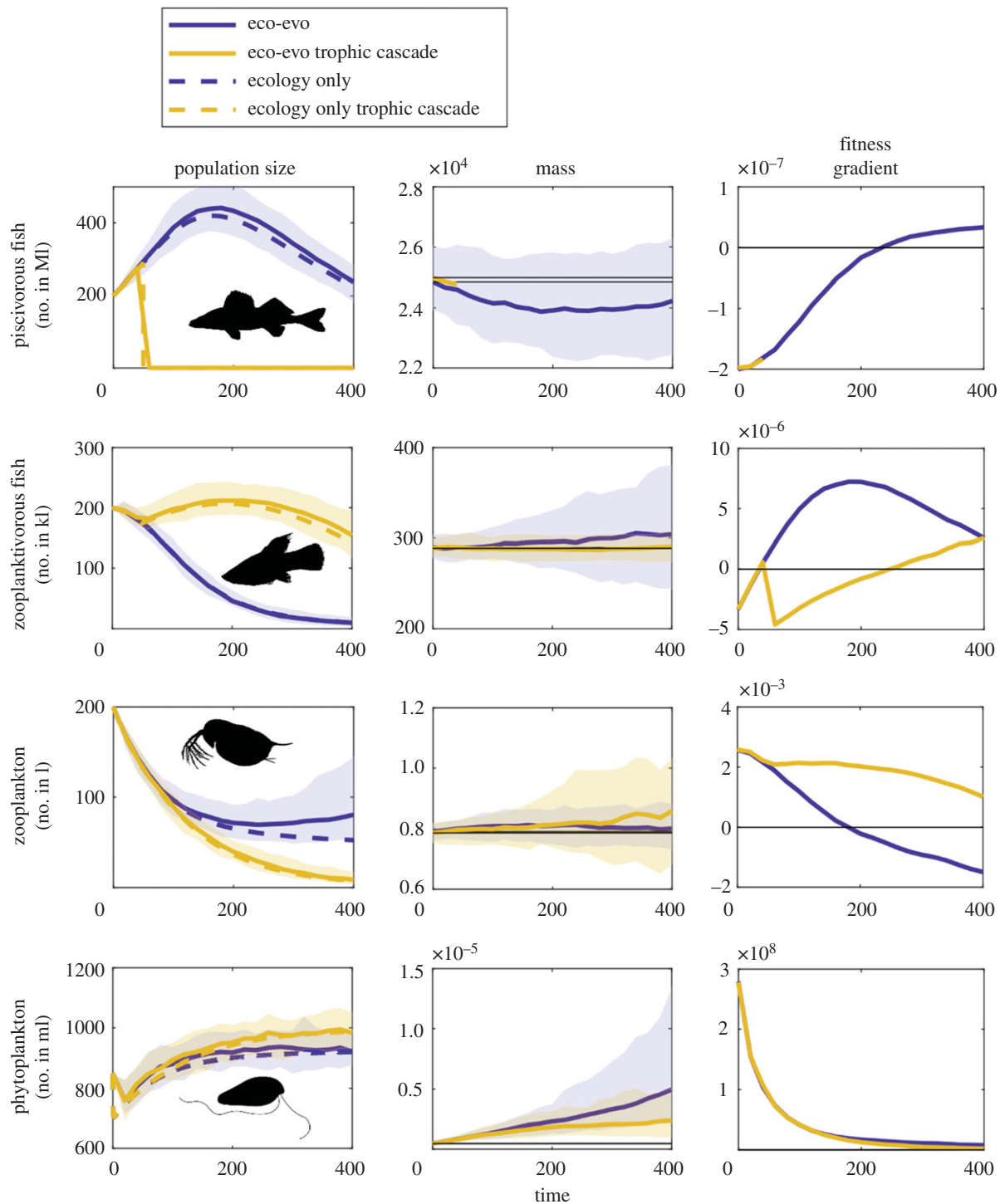


Figure 2. Eco-evolutionary dynamics of a four-trophic-level food chain model with negative prey mass scaling (functional response gets shallower with prey size). Abundances at each trophic level (left column) are shown for non-evolution ODE solutions (dashed lines) in the presence (yellow) or absence (purple) of a trophic cascade. Shaded areas show middle 50% of GEM simulations. Trophic levels are arranged from the apex predator (top) to the producer (bottom). Body mass (centre column) and body mass fitness gradients (right column) show selection and the potential for selection during trophic cascades. Negative values in fitness gradients indicate selection for smaller size and a positive number indicates selection for larger size. (Online version in colour.)

under higher predation pressure. For example, when piscivores were present, zooplanktivorous fish had wider 95% CI bands and trophic cascades widened bands of zooplankton (figures 2 and 3, centre column).

The loss of the top predator had cascading effects on the fitness gradients across trophic levels (figures 2 and 3, right column). Fitness gradients reflect how a per unit change in body mass impact fitness via changes in reproduction and mortality, and their switching reflects the flip-flopping of selection pressures across trophic levels consistent with trophic cascades [52]. When predators more effectively eat large prey

(positive scalings), fitness gradients approached 0 over time (lessening of selective pressure) as trophic levels experienced less predation pressure (e.g. zooplanktivorous fish and phytoplankton during trophic cascades). Under negative prey mass scaling, a similar pattern occurred for zooplankton. In general, changes in body mass across time and in response to trophic cascades were consistent with corresponding positive or negative fitness gradients (figures 2 and 3, right column) indicating that the net effects of abundances and body masses of both a particular species and that of its adjacent trophic levels led to changes in the direction and strength of selection.

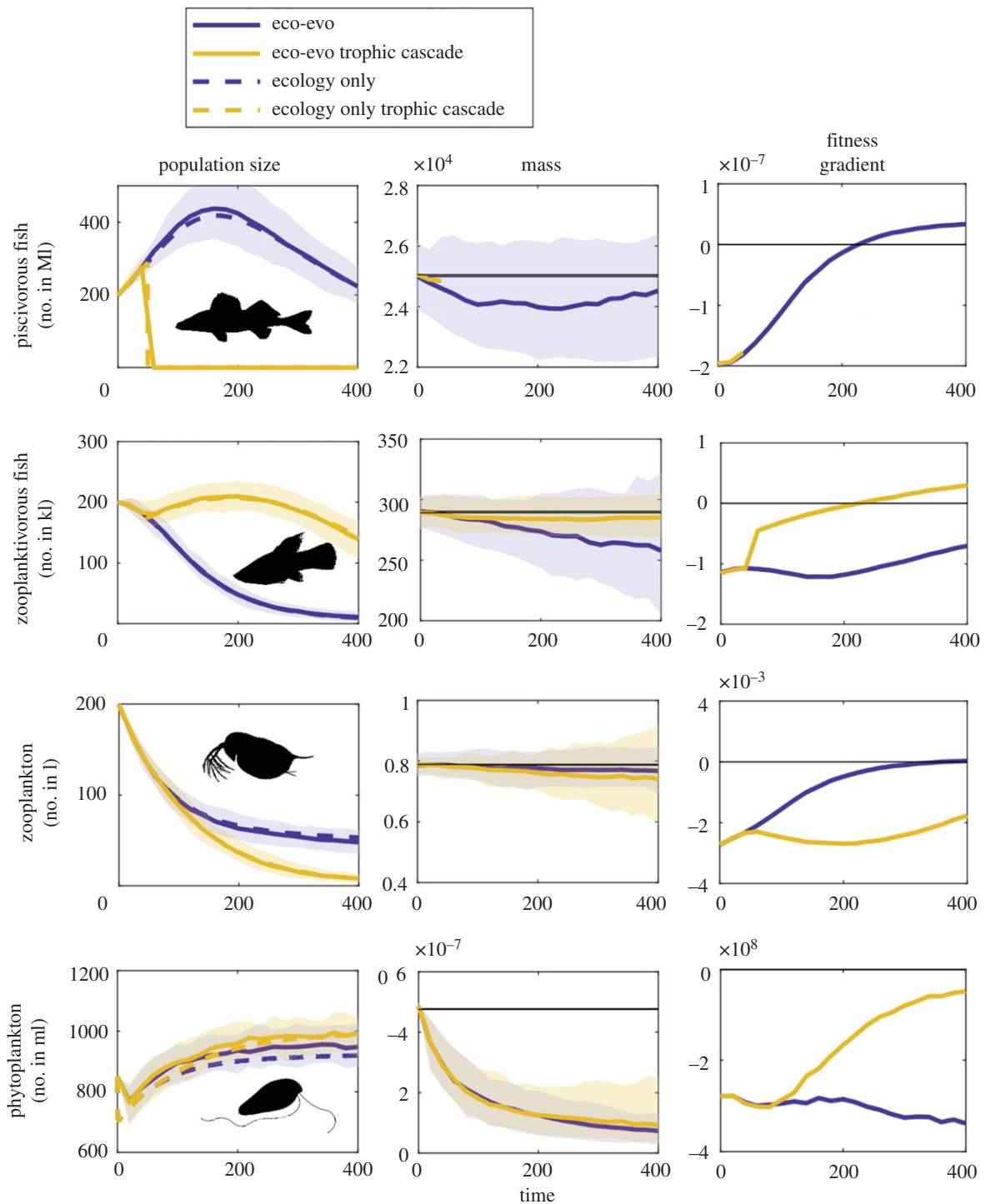


Figure 3. Eco-evolutionary dynamics of a four-trophic-level food chain model with positive prey mass scaling (functional response gets steeper with prey size). Figure layout as in figure 2.

Trophic cascades unfolded through the transient dynamics that emerged with the initial impact to the system. The loss of the top predator at day 50 induced a change in the zooplanktivorous fish, and this change took time to emerge. This lag influenced the timing of effects across trophic levels, causing divergence in trajectories to occur later at lower trophic levels (figures 2 and 3, left and right columns). Lags occurred for both abundances and fitness gradients, although the lag appeared to be greater for abundances than fitness gradients.

Generation times typically get shorter with smaller body size. Thus, our simulations covered more evolutionary time at lower than higher trophic levels. As a result, phytoplankton showed the greatest change in mass (relative to starting mass), even though they were the most distant from the top predator

and there was a lag in the propagation of effects to their populations. This is consistent with Wood *et al.* [11]'s prediction that generation time may change the time scale in which patterns emerge out of EETCs. Thus, populations with shorter generation times may still be the first to respond to altered eco-evolutionary dynamics even if they are more trophically distant from the perturbation.

4. Discussion

Trophic cascades are a key consequence of human-induced changes in the abundance of top predators. Whether through introductions, extirpations or harvest, changes in top predator

abundance alter the abundance, species composition, traits and behaviour of species at lower trophic levels [8,16,53,54]. Although trophic cascades may vary with habitat [17,55] or body size [18], or in some cases may be very difficult to detect [56,57], an underappreciated aspect of trophic cascades is that by changing abundances, trophic cascades also shift selection on traits that affect trophic interactions [11]. As a result, the underlying eco-evolutionary dynamics in the system will change, altering the trophic cascade itself. Our general depiction of this process (electronic supplementary material, appendix S1) suggests that any kind of trait linked to foraging interactions (e.g. body mass, competition, morphology or behaviour) will experience altered fitness gradients upon changes in top predator abundance. This will create a system in which trophic cascades induce alterations to predation pressure, changes in predation pressure alter fitness gradients of traits, and alteration of traits changes trophic interactions with that species's predators and prey. Such alternating changes across trophic levels also may interact with competitive effects, further altering the outcome [11].

Here, we showed that EETCs can arise across four trophic levels via body mass evolution, with alternating fitness gradients, trait change and shifts in abundance. Furthermore, the strength of the trophic cascade was diminished at the lowest trophic level. Moreover, our system is parameterized as an aquatic food chain, and aquatic trophic cascades are generally thought to be stronger than terrestrial food chains [17,58]. This difference suggests the possibility that aquatic trophic cascades in reality are not even as strong as they might be without the kind of rapid evolution that appears to be common in aquatic systems [7,50,51]. Finally, we observed a transient unfolding of the EETCs, with effects lagging in time for populations distantly removed from the initial impact to the top predator. In combination with other recent results [11], our results extend the discussion of eco-evolutionary dynamics, often focused on feedbacks between directly interacting species [50,51,59,60], to cascading effects to indirectly interacting populations [11,16], providing a potentially useful expansion of our understanding about how trophic cascades work. For example, EETCs may help us understand empirical patterns such as the different degrees of body size decline in fishes of different trophic levels in the northwest Atlantic [61].

EETCs were evident in our simulations as differences in the transient dynamics between scenarios in which body size did not evolve (ODE solutions) and those in which body mass did evolve (GEM solutions) (figures 1–3). Although these differences were not apparent at all trophic levels in both scaling scenarios, such transient behaviour [32] is particularly important to understand given that trophic cascades are often triggered by disturbances and managed at relatively short time scale. The EETC in our simulations showed different net effects through time and lags that initiated effects later at lower trophic levels, requiring a transient lens for understanding them. These changes across time were due to temporal shifts in both the direction and rate of change in size and abundance (e.g. the dotted lines in figure 1). Nonetheless, an equilibrium view indicates that interaction strengths between consumers determine the strength of a trophic cascade [18]. Interaction strengths depend largely on the functional response connecting predators to their prey, and our results point to declines in the space clearance rate (i.e. initial slope of the functional response) due to changes in body mass across the food chain. For example, we calculated that body

mass evolution increased the space clearance rate of zooplankton on phytoplankton by about 50% in the negative scaling scenario and decreased it by about 30% in the positive scaling scenario, indicating that the direction of change in traits can alter the strength of interactions and thus the nature of the resulting trophic cascade.

Although many traits could mediate the effects of trophic cascades, we focused on body mass because it is a critical life-history trait that evolves in response to predation risk, mediates predator–prey interactions and is linked to the strength of trophic cascades [17,18,25,26,62]. Body mass is also an ecologically pleiotropic trait with multiple effects on ecological function [63]; for example, body mass influences conversion efficiency, foraging, predation risk and mortality. As a result, how body size might mediate EETCs is difficult to predict, as the particular outcome depends on the net effect of body mass on multiple functions. Here, we used empirically well-grounded relationships between body mass and model parameters, but we bracketed the effect of prey body mass on space clearance rate with both a positive and negative scaling relationship. We chose this because larger prey might be more attractive by providing a large energetic reward or they might be increasingly difficult to capture. For example, functional responses of both water bugs (*Belostoma* sp.) and dragonfly nymphs (*Pantala flavescens*) foraging on red-eyed treefrog tadpoles (*Agalychnis callidryas*) got shallower with larger prey size [64]. By contrast, large backswimmers (*Notonecta maculata*) foraging on *Daphnia magna* showed steeper functional responses with larger daphnids [65]. Moreover, isopod functional responses varied with prey size differently depending on the size of the predator [66].

Our simulations also indicate that it is possible to have a mix of both clear eco-evolutionary dynamics and cryptic dynamics [67] at different trophic levels, even with pervasive body size evolution across trophic levels (figures 2 and 3). This may be due to the co-evolutionary nature of the dynamics, with prey evolving toward being consumed less and their predators evolving toward being able to consume prey more. Since cryptic dynamics occurred only at the level of zooplanktivorous fish in our results, however, we suggest that cryptic dynamics are just a special case where the ongoing changes in body mass lead to changes in births and deaths that cancel out, leaving no detectable difference between ecological and eco-evolutionary dynamics.

Some of the most staggering examples of trophic cascades come from systems where humans alter predator abundances [6,19,20,68,69]. The impact of these trophic cascades has long been associated with the change in abundances across trophic levels and, more recently, their attendant effects on ecosystem processes [3,8,9,70]. At the same time, research on predation- and harvest-induced changes to prey body mass has focused on changes in body mass of the harvested species [20,68]. Together with other recent modelling efforts [11], our results indicate that changes in top predator abundance can alter traits of species at lower trophic levels and induce a cascade of eco-evolutionary dynamics that alters the strength of the trophic cascade itself. Thus, some of the observed variation in the strength trophic cascades across systems [55,71] might be linked to differences in the potential for rapid evolution to cascade down focal food chains. Furthermore, the effect of trophic cascades on the function of microbial communities [9] may well involve both changes in abundance and traits of populations impacted by intermediate consumers. We suggest

that detecting the signature of EETCs might be easiest where populations with fast life histories (microbes, zooplankton) form the base of food chains. In summary, fully understanding the consequences of top predator loss will probably require understanding interacting changes in traits and abundance, and following the cascade across potentially numerous links in food webs.

Data accessibility. Code available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hx3ffbgb9> [72].

Authors' contributions. T.M.L. and J.P.D. conceived, designed, coded models, analysed model outputs and wrote the manuscript. Both authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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