Bifurcation or state tipping: assessing transition type in a model trophic cascade

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Abstract

Ecosystems can experience sudden regime shifts due to a variety of mechanisms. Two of the ways a system can cross a tipping point include when a perturbation to the system state is large enough to push the system beyond the basin of attraction of one stable state and into that of another (state tipping), and alternately, when slow changes to some underlying parameter lead to a fold bifurcation that anihilates one of the stable states. The first mechanism does not generate the phenomenon of critical slowing down (CSD), whereas the latter does generate CSD, which has been postulated as a way to detect early warning signs ahead of a sudden shift. Yet distinguishing between the two mechanisms (s-tipping and b-tipping) is not always as straightforward as it might seem. The distinction between "state" and "parameter" that may seem self-evident in mathematical equations depends fundamentally on ecological details in model formulation. This distinction is particularly relevant when considering high-dimensional models involving trophic webs of interacting species, which can only be reduced to a one-dimensional model of a tipping point under appropriate consideration of both the mathematics and biology involved. Here we illustrate that process of dimension reduction and distinguishing between s- and b-tipping for a highly influential trophic cascade model used to demonstrate tipping points and test CSD predictions in silico, and later, in a natural lake ecosystem. Our analysis resolves a previously unclear issue as to the nature of the tipping point involved.

Key words: tipping point, bifurcation, saddle-node, alternative stable states, trophic cascade, regime shift, trophic triangle

Introduction

Ecological systems prone to abrupt changes, such as a fishery collapsing, can be challenging to manage. These abrupt dynamics are often referred to as regime shifts, and result from nonlinearities in the underlying

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system dynamics. Therefore, ecologists have often turned to studying the dynamics of nonlinear but simple mathematical models to better understand and manage ecosystems. There are essentially two different mechanisms by which a system exhibiting alternative stable states can experience a sudden transition from one state to another (Scheffer et al. 2001): state tipping (S-tipping) or a bifurcation (B-tipping). Figure **??** illustrates these two mechanisms. B-tipping is a sudden transition that is induced by slow changes to a parameter of the underlying dynamical system that reduce the stability and ultimately destroy the stable node, as it collides with an unstable saddle-point in a saddle-node bifurcation (aka a fold bifurcation or "blue sky catastrophe," (Strogatz 2001)). In contrast, S-tipping involves a perturbation directly to a state variable that carries the system across the separatrix into an alternative stable state, without any such change to the underlying shape or existence of either attractor. S-tipping can be driven by direct exogenous forcing or purely stochastic events, such as extreme events that are common in the biological time series of ecosystems (Batt et al. 2017). Crucially, only one of these mechanisms, B-tipping, will exhibit the phenomenon of Critical Slowing Down (CSD), a pattern that has received great attention in both theoretical and empirical studies for its potential as an early warning signal of such a regime shift (e.g. Wissel 1984; Scheffer et al. 2009, 2015).

Despite this attention, convincing empirical demonstrations of critical slowing down are still rare, particularly outside carefully controlled laboratory settings (e.g. Dai et al. 2012). A foundational example can be found in studies of lake ecosystems (e.g. Carpenter et al. 2008), which can exist in either a "piscivore dominated" or "planktivore dominated" state (Figure 2). Significant previous work has established evidence for these alternative states and the potential for sudden transitions between the states that cannot be easily reversed. Then in 2011, a landmark study of Carpenter et al. (2011) analyzed the experimental manipulation of an initially planktivore-dominated state as a definitive example of CSD phenomena providing an early warning signal prior to a sudden transition to the piscivore dominated state. Yet was this manipulation truly an example of B-tipping, where CSD is theoretically predicted, or S-tipping, which does not create the CSD phenomenon?

B-tipping is typically considered to be the result of slow change in a parameter of (e.g. Scheffer et al. 2009) the system which ultimately leads to the fold bifurcation (or close enough to a fold bifurcation for stochasticity to finish the job). S-tipping involves manipulation of the state variable. Carpenter et al. (2011) describe driving the critical transition through the gradual addition of piscivores (largemouth Bass), which drives a transition characterized by low-piscivore density into one of high piscivore density. If the state (piscivore density) is being manipulated directly, then is this not an example of S-tipping, and thus

unsuitable to test for the presence of CSD? Although the simplicity of ball-in-cup (potential well) based descriptions of regime shifts makes them alluring, this question is impossible to address properly without a more mathematically precise description of the system and the manipulation involved. Surprisingly, despite the central importance the piscivore transitions have played in our understanding of ecosystem regime shifts, these details have never been clearly presented in prior publications. Here, we provide a direct analysis of the underlying model in the piscivory alternative state system to demonstrate why these studies are indeed an example of B-tipping.

Central to resolving this question is untangling a second issue that frequently arises in the discussion of alternative stable state dynamics in ecological systems: the issue of dimension. The S-tipping and B-tipping transitions illustrated in Figure **??** are fundamentally rooted in a one-dimensional analysis: the state consists of a single continuously valued dynamical variable (i.e. population density of adult bass). Ecosystems are notoriously more complex, and this lake ecosystem is no exception. Here, we analyze a previously published model of a trophic cascade to determine whether manipulating the top predator constitutes B-tipping or S-tipping. Common versions of this model include 5 state variables, ranging from top predators to primary producers (Figure 2). We perform dimension reduction on the full 5D model. This exercise facilitates the interpretation of the lake experiment in the context of predicting regime shifts by using a 1D model to understand a high dimensional system.

Methods

Model Description

In the model of the lake food web, largemouth bass (*Micropterus salmoides*, A) are the top predator. Intuitively, juvenile bass (J) mature into A, and J are produced by A. Bass feed on other fish, including their own young (J) and other planktivorous fish (F), (i.e. pumpkinseed sunfish, *Lepomis gibbosus* and similar forage fish species). These planktivores and juvenile bass (which are also planktivores) eat herbivorous zooplankton (H), which in turn eat phytoplankton (P). Because bass fry are small enough to be eaten by "planktivorous" fish, J can be consumed by F. Furthermore, F and J compete with each other for food (H). Thus, there are strong pairwise interactions between the three fish groups, and the dynamics of these groups extend into the planktonic portion of the food web. The five-dimensional model of the food web includes the aforementioned state variables consisting of three fish groups (A, F, J) and two planktonic groups (H, P):

$$\dot{A} = sJ - qA - m_A A \tag{1}$$

$$\dot{F} = D_F(F_o - F) - c_{FA}FA \tag{2}$$

$$\dot{J} = fA - c_{JA}JA - \frac{c_{JF}vJF}{h+v+c_{JF}F} - sJ \tag{3}$$

$$\dot{H} = D_H(H_R - H) + \alpha c_{HP}HP - c_{HF}HF \tag{4}$$

$$\dot{P} = r_P L \gamma(I_0, P)P - mP - c_{PH}HP \tag{5}$$

⁷²   Decreases in adult bass abundance result from mortality ($m_A A$) and harvest (q), and increases result

⁷³ from the maturation of the fraction of J that survive (s) mortality (Eq. 1). Planktivorous fish diffuse (D_F)

⁷⁴ between a refuge of size F_o and a foraging arena, and the predation rate of A on F is controlled by c_{FA} (Eq.

⁷⁵ 2). Growth in J is controlled by the fecundity (f) of A, but are subject to losses via cannibalization at a

⁷⁶ rate c_{JA}, and interactions with F which are controlled by the rate at which J hide (h) in a refuge or become

⁷⁷ vulnerable (v) to predation at a rate c_{JF} as they enter an implicit foraging arena (Eq. 3). Herbivorous

⁷⁸ zooplankton diffuse between surface waters and a deep water refuge (of size H_R) at a rate D_H, grow by

⁷⁹ preying on phytoplankton at rate c_{HP} and converting phytoplankton biomass (phosphorus) by a factor α,

⁸⁰ and decline as they are preyed upon by planktivores at a rate c_{HF} (Eq. 4). Phytoplankton death is due to

⁸¹ mortality and sinking at rate m or predation by herbivores at rate c_{HF}, while their growth is controlled by

⁸² the per capita growth rate (r_P), the availability of phosphorus (introduced at rate L), and the availability of

⁸³ light at the surface (I_0) and the density dependent growth response to phytoplankton in response to light (γ,

⁸⁴ Eq. 5).

⁸⁵   **Table 1.** Model parameters, description, values, and units. Parameters are taken from (Carpenter et al.

⁸⁶ 2008) and (Carpenter et al. 2013). The function γ describes phytoplankton growth, and can be found in

⁸⁷ (Carpenter et al. 2008).

Symbol	Description	Quantity	Units
q	Harvest or stocking	variable	t^{-1}
s	Survival rate of juveniles to maturation	0.6	t^{-1}
m_A	Mortality rate of adults	0.4	t^{-1}
m	Phytoplankton mortality	0.1	t^{-1}
f	Fecundity of adult bass	2	J/A
c_{FA}	Predation of planktivores by adult bass	0.3	$t^{-1}A^{-1}$
c_{JA}	Predation of juvenile bass on by adult bass	0.1	$t^{-1}A^{-1}$

Symbol	Description	Quantity	Units
c_{JF}	Predation of juvenile bass by planktivorous fish	0.5	$t^{-1}F^{-1}$
c_{PH}	Predation of phytoplankton by herbivores	0.25	$t^{-1}H^{-1}$
c_{HF}	Predation of herbivores by planktivores	0.1	$t^{-1}F^{-1}$
F_o	Abundance of planktivorous fish in non-foraging arena	200	F
H_R	Reservoir of herbivores in a deep-water refuge	4	H
D_F	Diffusion of planktivores between refuge and foraging arena	0.09	t^{-1}
D_H	Diffusion of between shallow and deep water	0.5	t^{-1}
v	Rate at which J enter a foraging arena, becoming vulnerable	80	t^{-1}
h	Rate at which J hide in a refuge	80	t^{-1}
r_P	Growth rate of phytoplankton	3	m^2mg^{-1}
L	Phosphorus loading rate	0.6	$mgm^{-2}t^{-1}$
α	Assimilation of phytoplankton phosphorus by zooplankton	0.3	gg^{-1}
γ	Density-dependent phytoplankton growth response to light	n/a	n/a
I_0	Solar irradiance incident on the surface of the water	300	$\mu Em^{-2}s^{-1}$

Dimension Reduction

Our approach to determining whether the lake experiment constituted B-tipping or S-tipping is to reduce the dimensionality of the model described in Eqs. 1-5, and see if a 1-D expression of this model can produce alternate states and the corresponding fold bifurcation. Although transitions occur throughout the food web, we focus here on the fish dynamics (Eqs. 1-3) as they are most directly related to either harvest (q) or direct manipulation of adult bass (A). In the model, the dynamics of herbivorous zooplankton (H) and phytoplankton (P) do not influence A, F, or J. Therefore, the dimensionality of the model can easily be reduced from 5 to 3 by ignoring Eqs. 4-5 (the plankton) without loss of generality for the dynamics of Eqs. 1-3 (the fish). In addition to parameters, the dynamics of each fish state depend on itself and at least one other fish state. We observe that the dynamics of both the Juvenile bass (J) and forage fish (F) occur on fast timescales relative to the dynamics of long-lived adult bass. Therefore, we set Eqs. 2-3 to zero and solved for the estimate of the respective state variables given equilibrium:

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$$\hat{A} = \frac{sJ}{q+m_A} \quad (6)$$

$$\hat{F} = \frac{D_F F_0}{D_F + c_{FA} A} \quad (7)$$

$$\hat{J} = \frac{fA}{c_{JA} A + s + \frac{c_{JF} v F}{h + v + c_{JF} F}} \quad (8)$$

The equation of motion for A (an expression of A's dynamics completely in terms of A and fixed parameters), is acquired by substituting the RHS of Eq. 7 for F in Eq. 8, then substituting the resulting expression for J in Eq. 1. After some substitution, we can write the equation of motion for the adult bass, A, completely in terms of the adult bass population and fixed parameters of the system.

$$\dot{A} = sfA\left(c_{JA} A + s + c_{JF} v \left(\frac{(h+v)(D_F + c_{FA} A)}{D_F F_o} + c_{JF}\right)^{-1}\right)^{-1} - qA - m_A A \quad (9)$$

Solving for the roots of this equation demonstrates alternative stable states and the potential for B-tipping with changing q, as illustrated graphically in Figure 4.

Simulations

We performed simulations in which we initialized the 5D model at equilibrium with a low but negative harvest rate ($q = -0.001$), which can be interpreted as per capita stocking of A. We proceeded to linearly increase q at each time step over 1020 years with a time step size of 0.01 years (102000 time steps total) until q reached a value of 0.001. At each time step a small amount of additive, normally distributed noise was added to Eqs. 1-3. Values for state variables less than 0.001 were set to 0.001 to prevent ecologically impossible values resulting from our numerical approximation of continuous dynamics. R code for these simulations is included in supplementary materials (<https://github.com/cboettig/bs-tipping>).

Results

Plotting this equation using established ranges for ecological parameters (Table 1; Carpenter et al. (2008); Carpenter et al. (2013)), Figure 4 shows that the system should support two alternative stable states, and can undergo a fold bifurcation (in reverse, creating a new stable point) when "catch" q is decreased sufficiently. This sudden transition is felt in other dimensions as its impact cascades down to the lower trophic levels.

These same dynamics can be seen in the direct numerical simulations of the full 5-dimensional model. At a q of 0, the fish in the simulation underwent a critical transition (Figure 4). This transition occurred during time step 510, although an abrupt change in state was not observed until step 850. The changes in A and J were similar, but were inversely related to those in F. The predation effect of A on J was small compared to

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the role of A's fecundity in producing J and A's role as a predator of F, which negatively impacts J as well. Overall, both bass time series decreased with increasing q (abruptly when stocking converted to harvest at $q = 0$), whereas the abundance of planktivorous fish was positively correlated with q.

The fish dynamics cascaded down to lower trophic levels, although H and P did not undergo abrupt transitions at the same time as the fishes. Instead, H and P exhibited strong nonlinear changes much earlier in the time series after q had increased only slightly. The small cumulative increase in q leading up to step 20 caused a slight increase in F and a dramatic decline in H (F's prey); after its initial decline, the abundance of H was 0.001 for the remainder of the time series. When H abruptly declined, P abruptly increased, then continued to increased approximately linearly for the remainder of the time series. Therefore, increasing q caused declines in both bass states (A and J), an increase in planktivorous fish (F), a decline in herbivorous zooplankton (H), and an increase in phytoplankton (P), a pattern consistent with a trophic cascade. All state variables exhibited abrupt state changes at some point in the time series.

Discussion

These results demonstrate that the system considered can indeed be driven through fold bifurcations as the parameter q is slowly tuned up or down (Figure 5), forcing the creation or annihilation of an alternative stable state – confirming the presence of B-tipping in this system. Simulations of the same system using previous estimates for ecological parameters confirm that the predictions of the 1-dimensional approximation (Eq 9) correspond with the dynamics observed in the full model.

This analysis also highlights the importance of what might appear to be a merely semantic issue that in fact corresponds to fundamentally different dynamics. In this formulation, the control parameter q corresponds to harvest (positive q) or stocking (negative q) of adult bass in the lake. It is this aspect that first gives the appearance of state tipping dynamics, since it suggests the state is being somehow "directly manipulated". Yet from a mathematical standpoint, it is irrelevant if the control parameter corresponds to some environmental or policy variable (fishing regulations, fish migration into the lake), which in turn increases or decreases net mortality proportionally, or if the manipulation directly adds or removes adult bass – the feature that distinguishes this manipulation from a S-tipping transition comes down to the timescales involved. Slowly increasing in the amount of bass stocked in the lake (i.e. decreasing q, effectively running the scenario of increasing fishing harvests in reverse) gives the rest of the food web time to adjust. In contrast, a single large introduction of many bass would create an S-tipping transition, driving the system immediately into an alternate state without exhibiting CSD phenomena needed to evaluate early warning signals of a

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tipping point.

All though we have focused on the analysis of deterministic models for simplicity, these results can easily be interpreted in the context of stochastic models as well. (Recall that in practice, the detection of early warning signals associated with CSD requires some level of stochasticity to generate the variance needed to detect slowing down). Under a stochastic model, the distinction between S-tipping and B-tipping is slightly blurred, since a system that gets close enough to the tipping point due to changing parameters (B-tipping) will ultimately be able to jump across the separatrix (S-tipping) before the actual bifurcation event. In a stochastic system, fluctuations in the state variable act as intrinsic sources of perturbations, and though part of the system, large chance deviations are no more predictable than sudden exogenous forcing: there is no CSD prior to purely stochastic transitions (Boettiger and Hastings 2013), even though retrospectively a large deviation will share similar statistical signatures such as rapidly increasing variance and autocorrelation (Boettiger and Hastings 2012).

More generally, our analysis draws attention to issues of dimensionality that have been largely overlooked despite significant interest in questions of regime shifts and early warning signals (e.g. Clements and Ozgul 2018; Scheffer et al. 2012, 2015). The popularity of this topic has sometimes led to casually equating any sudden shift with fold bifurcations, overlooking any assumptions necessary to approximate a complex dynamical system with such a one-dimensional model. Influential reviews on abrupt change in ecological systems (e.g. Ratajczak et al. 2018) focus almost exclusively on descriptions of one-dimensional state-spaces without discussion of if, when or how complex systems such as the ecosystem food-web considered here can be appropriately described by a nonlinear equation in a single dimension. The analysis shown here illustrates this process on the basis of a fast-slow timescale approximation, which allows us to replace the faster dynamics at lower trophic levels with their equilibrium states. (Note also that the nonlinearity necessary to support alternate stable states only emerges through this approximation.) Thus, for the five-dimensional model considered here, our analysis shows that the familiar one-dimensional characterization of a sudden shift being driven by a fold bifurcation is indeed appropriate, but this was not altogether evident a priori. The fact that CSD phenomena can occur in many different models has been suggested to mean that CSD is a generic or universal early warning indicator (Scheffer et al. 2009) of a critical transition. In practice, many higher dimensional models may not be so well approximated along a single manifold, or may correspond to other bifurcations or transitions (Boettiger et al. 2013). As such, analyses of regime shifts should not be too quick to sweep these details under the rug. Mechanistic understanding will always require models.

Acknowledgements

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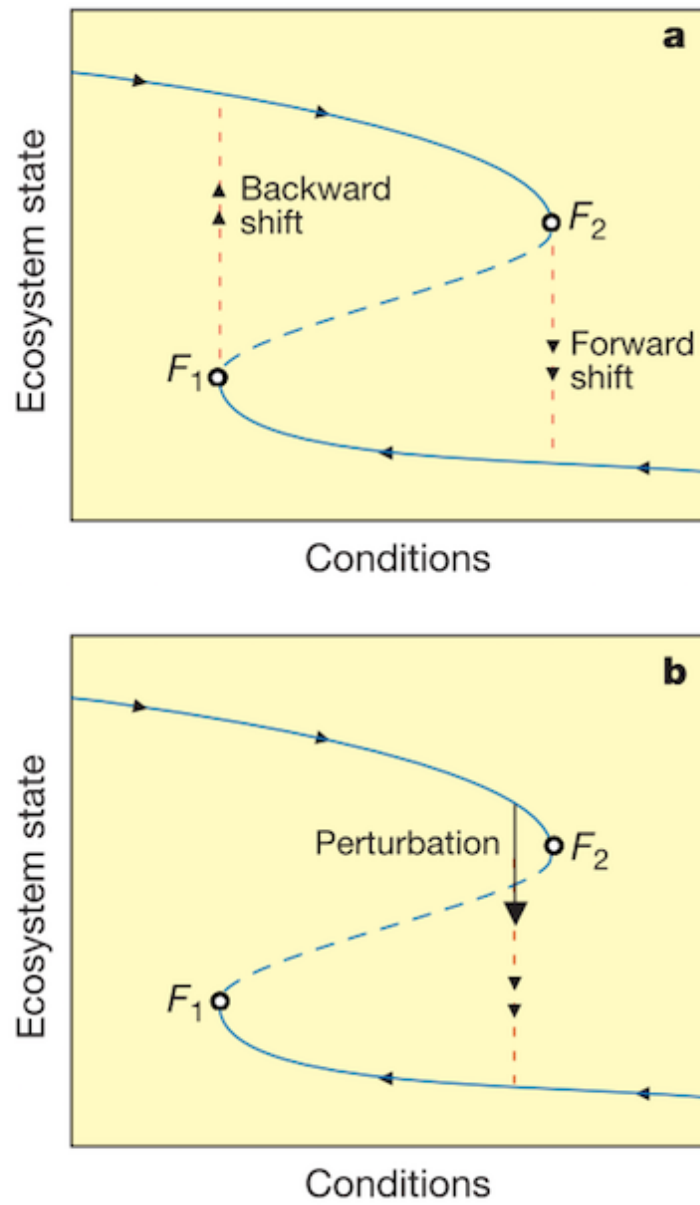
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Figure 1: S-tipping vs B-tipping. A critical transition in a system with alternative stable states can be driven either by a perturbation to the state, driving the system across the separatrix (top panel), or by a bifurcation, in which a stable point is annihilated (bottom panel). Figure reproduced from Scheffer et al (2001) with permission.
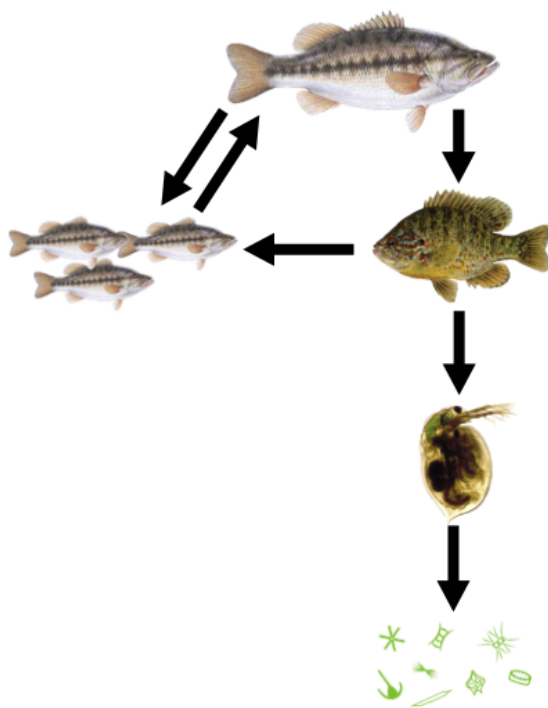
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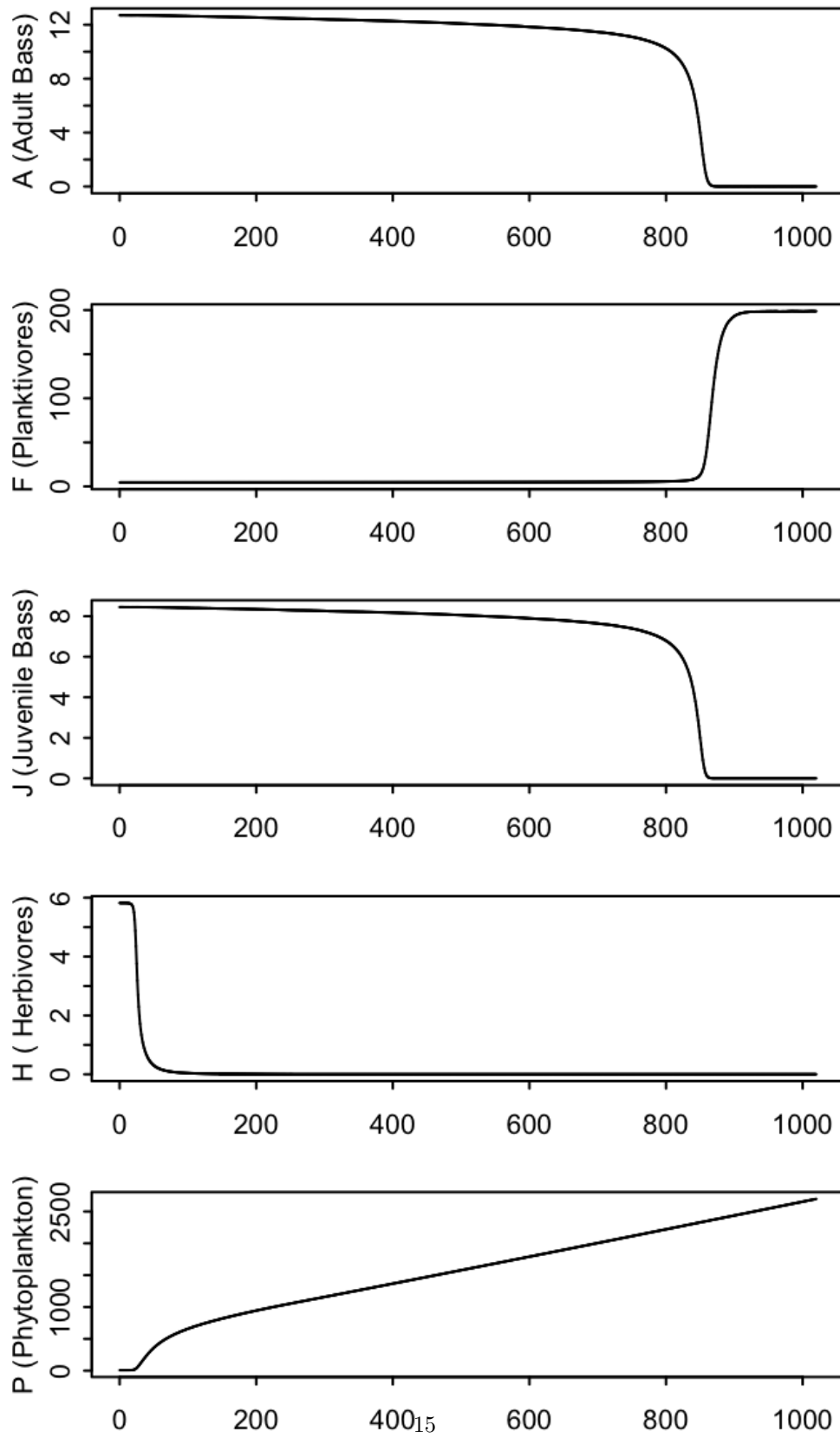
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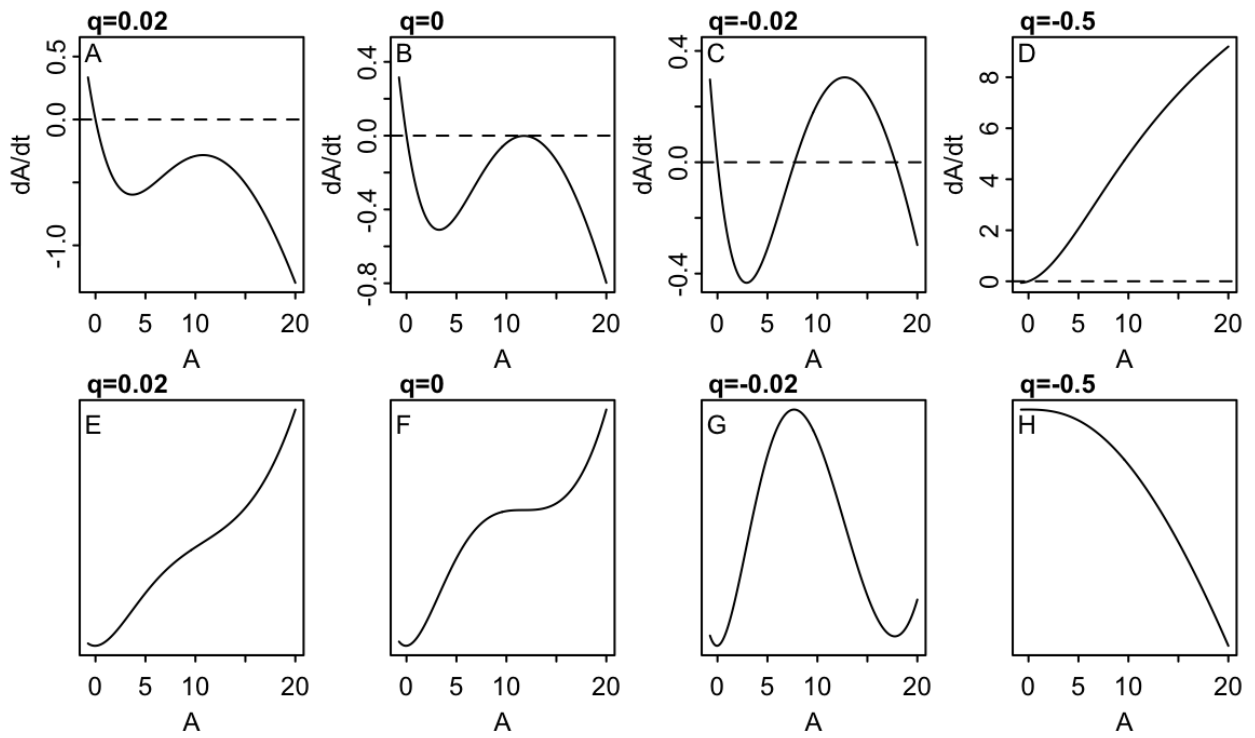
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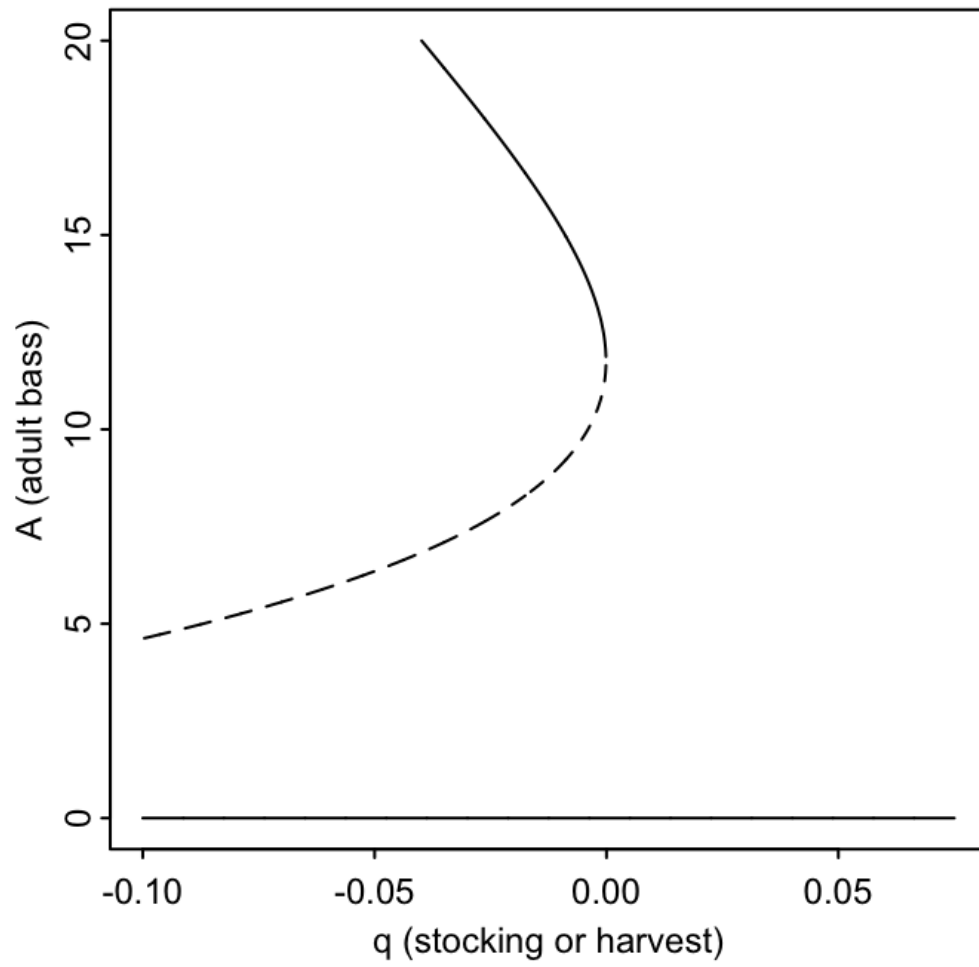
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