

A Review of the Trophic Cascade Concept Using the Lens of Loop Analysis: “The Truth is the Whole”^{1,2}

by

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Abstract:

Trophic cascades have been assigned an exaggerated even mythic status by some ecologists, but they are only one type of pathway in a complicated food web. The human mind is drawn to patterns like the proverbial ‘moth to the flame’. The distinctive checkerboard pattern of alternating + - + - + changes in populations on adjacent trophic levels in a trophic cascade is no exception. Unfortunately, this pattern has been too frequently equated with unrealistic ecological significance. Loop analysis, a qualitative network methodology, analyses all pathways and feedbacks in a food web simultaneously and it identifies many aspects of food web structure and function like trophic cascades, distinguishes operating from non-operating pathways, and predicts changes in standing crops and their correlation patterns. In this paper, the trophic relationships of food chains are expanded systematically into food web models that help illustrate some of the earliest claims about trophic cascades and their role in food webs. Several current definitions are contrasted to the loop analysis results. A more precise definition for a ‘top-down’ trophic cascade is proposed as well as the term ‘trophic escalade’ for particular types of ‘bottom-up’ trophic pathways that are also consistent with loop analysis. Suggestions for identifying trophic cascades are provided. Loop analysis, as an observing lens, provides an improved perspective on the role of trophic cascades. As Hegel claimed, “The truth is the whole”, and it cannot be found in an isolated part, in fact, the process of isolation precludes this possibility.

Key Words: Trophic Cascade, Trophic Escalade, Food Web, Loop Analysis, Keystone Predator

¹ Quotation from the German philosopher, George Hegel, (1807). In: “The Phenomenology of the Mind”. Preface: Paragraph 20. In German: “Das Wahre ist das Ganze”.

² Abbreviations: ATCH = Apparent Trophic Cascade Hypothesis, EEH = Ecosystem Exploitation Hypothesis, FW(s) = Food Web(s), GWH = Green World Hypothesis, KP(s) = Keystone Predator(s), LA = Loop Analysis, PI(s) = Parameter Input(s), TC(s) = Trophic Cascade(s), TDC = Trophic Dynamic Concept, and TE(s)= Trophic Escalade(s)

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1.0 Introduction

Trophic dynamics has been an important focus throughout the history of ecology beginning with Darwin's (1859) notion of the tangled bank (Forbes, 1887; Elton, 1927; Odum and Odum, 1953; Lindeman, 1942; McIntosh, 1985; Golley, 1993; Layman, et al. 2015). Fretwell (1987) concluded that the theory of the food chain dynamics is so fundamentally important to ecology that it rivals the theory of evolution. In this tradition, Terborgh and Estes (2010) concluded "that trophic cascades are the key to understanding how ecosystems function. And if this should prove true, ecology will finally have found its Holy Grail: the power to predict the responses of ecosystems to many kinds of abiotic and biotic perturbations". Ripple et al. (2016) concluded, "few concepts in ecology have been so influential as that of the trophic cascade...[and it is]...an idea that represents one of the foundations of modern ecology".

Trophic cascades (TCs) were first observed in nature. Leopold (1949) suggested that extirpation of the wolf would have ecosystem effects in the southwestern United States; Hrbacek et al. (1961) reported changes in plankton populations caused by freshwater fish predators in Czechoslovakia; and Paine (1966) demonstrated abundances in prey populations could be manipulated by starfish predators in the rocky intertidal zone of the Pacific Northwest. Paine (1969) named this apex species: 'keystone predator' (KP). He first used the term 'trophic cascade' (TC) in 1980 when describing how changes in KPs such as starfish, sea otters and lobsters at the top of the food web (FW) caused 'cascading effects' to lower levels (Paine, 1980). While he did not give a precise definition of the term, he likened a TC to a "series of nested strong interactions" that emulate from changes in a KP. More recently, he used the Power (1992) definition: "a keystone regardless of its phyletic affiliation can be recognized by an effect on its community disproportionate to its abundance or mass". Paine focused upon the functional roles of species rather than trophic levels, which he believed were at best a 'convenient' oversimplification since many species "cannot be assigned to any single level" (Paine, 1980). Thus, in his early work his emphasis was not on the TC per se, but rather identifying the cascading effects caused by predators was a way to analyze their functional role and importance in an ecosystem. Since then, a variety of authors have proposed diverse definitions of TCs (Ripple et al., 2016)⁴.

The purpose of this paper is to critically review several definitions and concepts that frequently appear in TC studies and evaluate them by analysing some examples and insights from LA, a qualitative network technique (Lane, 2016; In Press). The five loop models included here are related to earlier studies that significantly influenced current TC thinking. They are organized to make a systematic progression in FW complication. LA facilitates the focus on qualitative FW structure to understand FWs without the preoccupation with quantification. The technique provides information on the most likely

⁴ For the purposes of this paper, the following definition based upon LA is used: *A trophic cascade (TC) is all or part of an operating pathway, including at least three adjacent variables, starting with a variable at or near the top of the food web and ending with a variable at the bottom, with all the links on the pathway representing predator-prey and consumer-resource interactions that produce a checkerboard pattern (+ - + or - + -) of changes in the standing crop of the path variables.* (See also Section 3.1 for more explanation).

parameter input (PI) or driving force, all possible links between variable pairs both trophic and non-trophic, main operating pathways of effect, and a variety of structural and functional measures of FWs (Lane, 2016). It is also an excellent tool to identify a specific operating pathway like a TC and its role in relation to the whole food web.

Harvard ecologist and creator of LA, the late Richard Levins, was fond of quoting Hegel's "*Das Ganze ist das Wahre*" or "the truth is the whole". It was the guiding principle of his highly creative and productive career. It should also guide us in considering the TC concept. TCs emerge from the structure and function of whole ecosystems and cannot be understood as extracted bits such as a single predator, however voracious, or in the case of humans, a single species, however destructive. In a FW, there can be dozens of feedback loops acting simultaneously along multiple pathways and an array of environmental inputs that constitute both support for and stress upon ecosystem integrity. LA enables one to envisage this myriad of feedback relationships operating simultaneously in a FW, thus providing a rich observational and analytical potential. Consideration of the whole is also imperative when designing and selecting management options for degraded ecosystems. I believe the whole comes into better focus with LA as compared to many reductionist approaches.

2.0 Methods

LA is a signed digraph methodology created by Richard Levins (1973, 1975); the underlying mathematics and applications have been elaborated in several papers including Lane and Levins, 1977; Puccia and Levins, 1985; Lane, 1986a,b; Wright and Lane, 1986; among others. This qualitative methodology enables ecologists to construct FWs either (1) using only their ecological intuition or (2) by fitting data. In this paper, the loop models are hypothetical and of the first type. They include a set of variables connected by signed (+ or -) two-way links; some of these variables have been called 'trophic species' (Yodzis and Winemiller, 1999; and Williams and Martinez, 2008) or functional groups by other authors. When the link ends with a small arrow-head it has a positive effect on the variable it touches, and when the link ends in a small circle-head it has a negative effect on the variable it touches. There are nine possible link types that can represent all conventional density-mediated trophic interactions as well as one-way and two-way non-trophic interactions resulting in maximum flexibility in representing interactions found in nature. The total set of links can be represented by a matrix, which is equivalent to the traditional Community Matrix of alpha values given in qualitative terms (Vandermeer, 1990; Levins, 1968). Once a loop model is constructed, it can be dissected into its paths and loops. Paths begin at one variable, and then enter and leave each other variable on the path just one time each until reaching an end variable. Loops are closed feedback paths that return to the original variable, that is, feedback is the effect of a variable on itself by way of intervening variables. Both paths and loops are calculated by multiplying the algebraic signs of their links. Paths of K variables have K-1 links and loops of K variables have K links.

Using LA, one can predict qualitative changes (+, -, and 0) in standing crops and turnover rates of all variables (N) in a FW associated with a PI using the calculation equations in Levins (1973, 1975). PIs are external pressures or drivers that impact the FW at a given node as either + or - like the driving forces used in systems analysis and not as the diverse uses of the term discussed by Oesterwind et al. (2016). PIs, as initial perturbations to the FW, change the parameters of a species' growth equation, which can

change the standing crop or turnover rate of the original variable that is impacted. This impact can travel through various pathways to some or all other variables with resulting changes in their standing crops and turnover rates, but PIs do not usually change the network structure *per se*. Paths are ‘operating’, only if the variables not on the path are contained in one or more disjunct loops that form a valid complement. Operating paths or ‘pathways of effect’ are critical to understanding how food, energy, and information move around the FW. A potential TC is only one to a few such possible pathways in a single FW, and like any pathway, may or may not be operating.

LA can also systematically enumerate all paths and loops as well as calculate their signs for all possible lengths including 0: a path of length 0 is +1 and a loop of length 0 is -1. Puccia and Levins (1985) provide easy-to-follow calculation examples. Mathematically there are N^2 standing crop predictions for all positive PIs and an equal number associated with the negative PIs for each variant of model structure (A and B) in Figures 1-3 with N = the number of variables. If there are multiple pathways from a PI to a variable that involve different signs, then the prediction is ambiguous, which is indicated by a “?” in a table of predictions termed the ‘Community Effects Matrix’. This is also a square matrix, but the set of changes associated with the particular PI are read across the rows. Resolution of ambiguous predictions using semi-quantitative analysis is described in Lane and Levins (1977). For example, there can be three positive pathways and one negative pathway, but this does not mean that the final effect is positive. The dominant result is a function of the strengths of the links involved.

Given the standing crop predictions, it is possible to determine correlation signs between pairs of variable changes also across the rows of the prediction matrix (Community Effects Matrix) associated with a given PI as well as overall correlation patterns for the whole FW. LA also facilitates many measures of structure and function in FWs (Lane, 2016). Among these, the most relevant ones to this discussion are: position of key features such as self-damping terms, connected food chains or tiers, one-way links, and satellite variables all can affect feedback relationships (Lane, 2016).

3.0 Results and Discussion

First, simple one-tier food chains with potential TCs are modelled using LA to achieve some initial definitional clarity. Where appropriate, parallels are drawn with early trophic studies such as: Trophic Dynamic Concept (TDC) (Lindeman, 1942), Green World Hypothesis (GWH) (Hairston, Smith, and Slobodkin, 1960) and the Ecosystem Exploitation Hypothesis (EEH) (Oksanen et al., 1981; Fretwell, 1987; Oksanen and Oksanen, 2000). In Section 3.2, two-tier food webs are illustrated such as Paine’s (1980) Keystone Predator Concept and Polis’ Apparent Trophic Cascade Hypothesis (ATCH) (Polis et al., 1997; Polis et al., 2000).

3.1 Food Chain Models

Figures 1-3 illustrate food chains containing 3-5 variables. Tables S1-S3 include the predictions for standing crops and their correlation patterns for these models. Valid pathways are most obvious in food chain models and can only flow in a straight line up or down a food chain so they are not individually discussed or listed for Figures 1-3. As the loop models become more complicated, predictions and correlations are given in a condensed form to save space. To avoid redundancy, initial observations are not repeated although many continue to apply as the models become more complicated. In each figure, there is no self-damping shown at the top trophic level (model variant A), however, its potential ramifications are discussed as model variant B, which has self-damping, but is not illustrated. Self-damping, the negative feedback of a variable on itself, is described in Lane and Levins (1977). These short negative loops of length 1 enhance model stability. At the top of the FW, self-damping can occur through cannibalism and parasitism, or predation that is external to the FW. For example, effects of predators such as fish, seabirds, marine mammals, and humans that do not appear within the set of variables in a plankton loop model can be embedded in self-damping terms or they can function as PIs.

Figure 1. Community Effects Predictions and Correlations for Figure 1: a Three Trophic Level Food Chain with One Nutrient (N_1), One Algal Group (A_1), and One Herbivore (H_1). Model Variant A with no self-damping on H_1 is as shown. Model Variant B with H_1 self-damped is not illustrated. Predictions are given for all possible positive and negative parameter inputs numbered 1 to 6 for both variants A and B. See Table S-1.

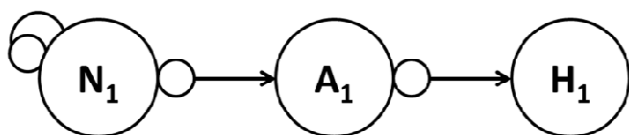


Figure 2. Community Effects Predictions and Correlations for Figure 2: a Four Trophic Level Food Chain with One Nutrient (N_1), One Algal Group (A_1), One Herbivore (H_1), and One Carnivore (C_1). Model Variant A with no self-damping on C_1 is as shown. Model Variant B with C_1 self-damped is not illustrated. Predictions are given for all possible positive and negative parameter inputs numbered 1 to 8 for both variants A and B. See Table S-2.

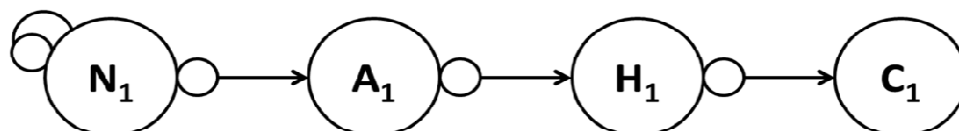


Figure 3. Community Effects Predictions and Correlations for Figure 3: A Five Trophic Level Food Chain with One Nutrient (N_1), One Algal Group (A_1), One Herbivore (H_1), and Two Carnivores: a Mesopredator (C_1) and an Apex Predator (C_{1^*}). Model Variant A with no self-damping on C_{1^*} is as shown. Model Variant B with C_{1^*} self-damped is not illustrated. Note: the negative parameter inputs are deleted here, but their standing crop predictions can be imagined by flipping the signs for the corresponding model from a positive parameter input to a negative one. Correlation patterns remain the same. See Table S-3.

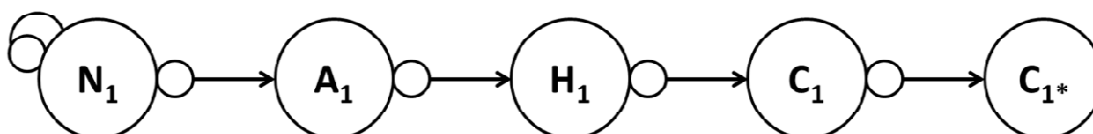


Figure 1 is a small three variable food chain like the early example of Charles Elton's (1927) study of the Canadian lynx, snowshoe hare, and a plant. Leopold's (1949) shrub-deer-wolf food chain is another example. Figure 2 illustrates the four-variable food chain and it is reminiscent of the Hairston, Smith, and Slobodkin's (1960) Green World Hypothesis (GWH), which was a conceptual top-down model that further added to the popularity of the notion that changes on one trophic level could affect other ones even if they were not adjacent to each other (indirect effects). This small paper sparked a large debate over how populations are 'controlled' in nature. The two opposing viewpoints were termed the density-dependent and density-independent approaches. Interestingly, the opponents agreed on the same three basic assumptions: (1) fossil fuels do not accumulate; (2) the world is constantly green; and (3) therefore, herbivores (H) are not limited by food supply. They also both agreed-upon the use of generalized trophic levels, grouping many species together based on their food sources and predators while ignoring the problems posed by omnivores, detritivores, and their interactions. This conceptualization is problematic. For example, Polis and Strong (1996) like Paine concluded the trophic levels do not exist. Murdoch (1966) also believed that trophic levels were at most an abstraction that never could be measured, although the International Biological Program certainly attempted to do that in the 1970s. Some have suggested that guilds and trophic levels are interchangeable, however, Oksanen and Oksanen (2000) have concluded this is 'conceptually debatable'. They found they had to relax the assumption of homogeneity of trophic guilds to explain their EEH for terrestrial ecosystems.

Even more interesting, after adopting the same conceptual base and assumptions, proponents of each approach then formulated a different conclusion. The density-dependent camp, as per Hairston, Smith and Slobodkin (1960), assumed that herbivores were not limited by weather, but by predators, while in contrast, the density-independent camp championed by Andrewartha and Birch assumed that herbivores are not limited by predators, but instead by weather. Undoubtedly, their different study organisms also shaped their notions of population 'control'. Andrewartha and Birch studied delicate thrips living in rose gardens whereas Hairston worked on salamanders, parasites and

pathogens, and Slobodkin and Smith studied *Daphnia* and other aquatic organisms known for their competition and predator-prey interactions.

LA can help distinguish the possible validity of various hypotheses. For example, the density-independent opponents held a conceptual view like Figure 1 in which C did not even have to be present in the food chain, but even if it was as in Figure 2, the location of the abiotic PI as a negative input to H via a weather impact was the most important feature of H's 'control' as in Table S1, PI Nos. 5A, 5B, 6A, 6B, and in Table S2, PI Nos. 7A, 7B, 8A, and 8B. The loop model predictions agree with the classic top-down TCs consistent with the GWH of Hairston, Smith and Slobodkin (1960) whereas predictions for a negative PI at H in Models 1 and 2 do not agree with the density-independent hypothesis. The density-dependent school supported a Figure 2 viewpoint with an additional predator level, C, being necessary for their conclusion. In the latter viewpoint, it was C that 'controlled' H and not a negative PI to H. The negative link from C to H decreased H as per predictions 7A and 7B in Figure 2A, although it required a PI to C to activate the C-H interaction. Thus, to Hairston, Smith and Slobodkin (1960), the most important PI was a positive one to the carnivores (C). When environmental conditions were better for C, H suffered and was 'controlled'. They apparently disregarded the equally-likely situation that life could deteriorate for C (predictions 8A and 8B for a negative PI to C) and H would increase and consume more plant matter.

The GWH debate continued for decades despite the assumptions not proving to be as robust as first suggested. For example, some fossil fuels accumulate and the world is not all green, but also blue, brown, and white. Over time, the argument narrowed to a question of how terrestrial herbivore abundances were regulated, but it was still a broad inquiry. Hairston, Smith, and Slobodkin (1960) made several expansive assumptions and conclusions on the basis of a few over-simplified trophic levels. Simplification can be good and often necessary in ecology, but not beyond the point where it obfuscates reality. Essentially, the GWH was a debate over the sign (+/-) of the dominant PI and where it entered the FW. Underlying this logic, were the assumptions that there was only one dominant PI and it remained constant in perpetuity. This problematic assumption is frequently made in the current TC literature. Furthermore, Hairston, Smith and Slobodkin (1960) assumed that PIs as external drivers could 'control' species if not whole trophic levels and what was being 'controlled' was population abundance, which was the most important feature even though many evolutionarily-successful populations appear to be selected for low abundance and high variability. This early notion of control in food chains has also been touted enthusiastically, but imprudently as a management tool for natural ecosystems (Worm and Paine, 2016). There have been continued efforts to support one approach or the other to the present with subsequent field studies (Terbough, et al., 2006; Terbough and Estes, 2010).

Polis (1999) compared the GWH with the EEH, which suggested that the world is green in systems of one or three trophic levels, but there is little green in systems with two or four trophic levels. LA results do not generally support this conclusion; the number of trophic levels and whether it is odd or even, is not as important as the specific food web structure. An additional difficulty in numbering trophic levels is whether the nutrient level is explicitly represented in the FW or not; LA results to date indicate that the nutrient variables play a key role in the overall structure of the ecosystem, but they are often

omitted. The EEH also depends on strong consumptive capabilities at each level on the next lower adjacent one. Polis (1999) presented six hypotheses on herbivore regulation of plants, but only one involved the GWH and EEH, which both required three key interactions to operate simultaneously in a FW: (1) herbivores depress plants, (2) predation depresses herbivores, and (3) predators indirectly facilitate plants. PIs were also not properly accounted for in the EEH. He concluded that it is unlikely that either the GWH or the EEH is a realistic explanation for population control in nature since both rely on too many coarsely-lumped trophic levels and too many conditions. LA supports this conclusion. In addition, PIs to the carnivore levels in Figures 1-3 indicate that the checkerboard pattern of alternating signs in adjacent trophic levels is not mysterious and can be commonplace in many FWs.

Figure 3 denotes a five-variable food chain. In simple models like this one, it is often possible to determine turnover rates, which can easily be inferred by observing the changes in standing crops of adjacent variables in the Community Effects Matrix. For example, is there a positive PI at the nutrient level, N_1 , H_1 and C_1^* increase, but there is zero change in the standing crops of A_1 and C_1 . This indicates that the latter two variables have increased turnover rates in that the biomass being produced at one level is passed directly to the predators of the next higher trophic level. Both Figures 2 and 3 also depict two different views of the Trophic Dynamic Concept (TDC) advanced by Raymond Lindeman, usually without the nutrient level. Note: N_1 could be omitted in any of these models, but then its self-damping would be transferred to A_1 (Levins, 1975). Only positive PI predictions are given, however, the negative PI predictions are simply reversed (+ to – and – to +), that is, flip signs, for PIs to the same nodes. For example, in Table S3, the five sets of predictions for negative PIs are not listed, but can be easily determined by the reader.

A description of the correlations associated with the standing crop changes is given in the right-hand columns of Tables S1-S3. If only the sign of the PI changes at a node, the resulting correlation patterns remain the same. Thus, the only changes in the correlation patterns shown here are related to changes in the location of the PI. In terms of mathematical possibilities, there are $(N^2-N)/2$ possible correlation coefficients for each number (N) of variables. For example, if N equals 8, then there are 28 possible correlation coefficients among the variable pairs, however, some are often zero. Even with these very simple food chain models, patterns of correlation can be highly variable although the FW structure remains invariant in each of the models since only the PI location changes. There are three sets of unique correlation patterns among the three variables for each model variant (A and B) for Figure 1 and five sets for Figure 2 even though these two models are only one variable different in size. By adding a fifth variable, Figure 3 exhibits eight sets of correlation patterns. Thus, distinct sets of correlation patterns can increase exponentially as N increases. Furthermore, no ecosystem in nature exists as a food chain of only three to five variables. For simple food chains, however, these results provide a convenient template of directed changes in the abundances of species and/or trophic levels and their correlation patterns, which can be compared to field and lab data. This comparison can be useful both in determining whether the trophic structure has been accurately conceptualized and to identify the most likely locations for PIs that produce the observed community-wide changes in the standing crops of all variables.

3.2 Food Web Models

Figure 4 portrays two food chains of five variables each that are linked at the nutrient-algal levels (Figure 4). Figure 5 is like Figure 4 except that there is only one apex predator (C_1^*) that consumes both meso-predators (C_1 and C_2), thus linking the two food chains into one FW. These figures assume no omnivory, which is not a realistic assumption for most ecosystems. In Figure 4, there are approximately two pathways for most PIs starting in the bottom tier (tier 2) and about three pathways starting at the top tier (tier 1). This is because there is only one path to get to the top from the bottom, but the top has two pathways to get to the bottom because of the one-way arrows. There are also more paths in Figure 5 despite having fewer variables than Figure 4. Of structural interest in both Figures 4 and 5 is the presence of luxury consumption by A_1 . This is a one-way link that partially restricts tier 2 from affecting tier 1. One-way links can have a profound effect on network structure often more than the presence or absence of a given KP. There were several instances of apparent top-down TC canonical correlation patterns, however, some of these originated in the lower parts of the FW, went up to the apex predator and down the other tier.

Figure 4. Two Linked Food Chains Each with Five Trophic Levels Sharing Nutrients N_1 and N_2 . Algal group, A_1 , is a luxury consumer of nutrient N_2 whereas A_2 is not. The apex predators, C_1^* and C_2^* , are both self-damped. There are two herbivores (H_1 and H_2) each with a preferred food (A_1 and A_2 respectively). Two meso-predators (C_1 and C_2) are consumed by two apex predators (C_1^* and C_2^* respectively), which are both self-damped. Note: the negative parameter input predictions are deleted here, but can be imagined by flipping the signs for the corresponding model with a positive parameter input at the same node. Rows labelled 'result' are the summation of multiple paths that have at least one difference in prediction. A "?" is entered when there are both + and - predictions for the same input node. Only the minimal sets of paths needed to reach all variables are given in the key below by input node; they subsume smaller paths of a fewer number of variables. Individual paths are separated by the underlined word 'and' in the key below.

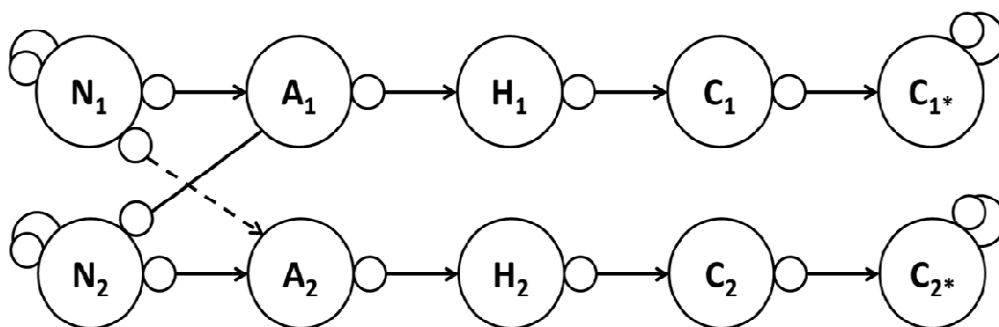


Figure 5. Two Linked Food Chains Each with Five Trophic Levels Sharing Nutrients N_1 and N_2 as well as C_{1^*} , an Apex Predator. Algal group, A_1 , is a luxury consumer of nutrient N_2 whereas A_2 is not. There are two herbivores (H_1 and H_2) each with a preferred food (A_1 and A_2 respectively). Two meso-predators (C_1 and C_2) are consumed by the apex predator, C_{1^*} , which is self-damped. Note: the negative PIs are deleted here, but can be imagined by flipping the signs for the corresponding model with a positive parameter input. Rows labelled 'result' are the summation of the directed change predictions for multiple paths. A "?" is entered when there are both + and - predictions for the same PI node.

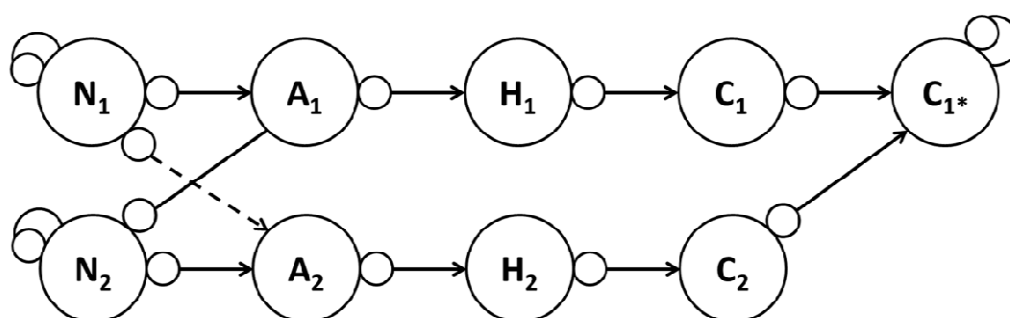


Table S4 gives the community effects predictions for Figure 4 for all positive PIs. When there are multiple operating pathways for a PI, the overall result is given in the row labelled 'Result'. Notice that there are some question marks or prediction ambiguities in Table S4 since there is now more than one pathway between some PIs and their end variables, especially involving the nutrient level, which was not possible in the simple food chains (Figures 1-3). Table S5 contains selected sets of the longest operating paths in Figure 4, which illustrates some combinations of the multiple pathways that can lead to prediction ambiguity. There are also many potential pathways that are not valid and not operating in this network because the variables not on the pathway are not in valid complements. There are 3^{100} or $10^{47.71}$ mathematically possible FW structures for a ten-variable FW such as Figure 4 and 3^{45} possible patterns of correlation for the three possible values of directed changes for standing crops (+, 0 and -).

Although not exhaustively, enumerated here, Table S6 contains ten different correlation patterns in the changes in standing crops of the ten variables for only a single FW structure in Figure 4 with the potential PIs at each of its ten variables (Figure 4). Furthermore, if the standing crop prediction is ambiguous, then any correlation value including that prediction is also ambiguous. As the predictions in standing crops become more ambiguous, so do the correlation patterns. In total, there are 16 ambiguous predictions in the 'Result' rows. Wherever ambiguity occurs in the model predictions, resolution difficulties will be magnified in the field when investigators attempt to determine the presence or absence of trophic cascades.

Table S7 contains the community effects predictions for Figure 5, which involves one-fewer variables (9) and Figure 4, but connections between tiers occur at both the

bottom and top of the two food chains. This facilitates more multiple pathways between PIs and variables. There are 44 question marks in Table S7 in the 'Result' rows, but no zeros in the predictions for both Figures 4 and 5. This is because the terminal variables are all self-damped in the networks so that each path has a valid complement. Table S8 summarizes the correlation patterns in standing crop predictions for a positive PI to each of the nine variables and the set of multiple pathways associated with each one, which is labelled 'R'. The results (R) only capture the non-ambiguous correlations whereas individual pathways mostly include all variables and their correlations. Without further quantification, however, we don't know which pathway will dominate in nature. Although more complicated than Figures 1 to 3, Figures 4 and 5 are also causally impoverished. In comparing them to each other, Figure 4 has 10 variables and Figure 5 has 9, but the latter figure connects the 2 food chains with an apex predator and thus, it is possible to travel from tier 1 (top) to tier 2 (bottom) or tier 2 to tier 1 without going through nutrients. This increased connection of the 2 tiers results in more prediction ambiguity.

Both Figures 4 and 5 are reminiscent of earlier studies by Paine (1966, 1969, and 1980) on the role of the KP in the rocky intertidal zone and Polis' formulation of the Apparent Trophic Cascade Hypothesis (ATCH) (Polis, Anderson, and Holt, 1997; Polis et al. 2000). Paine was primarily interested in constructing 'functional FWs' that were derived from experimental manipulations, especially of predators such as starfish, and identifying the effects of their interactions in their FWs. He distinguished his models from those based upon connectivity *per se* and nutrient-energy transfer. To Paine, functional role was closely related to whether a change in the density of one species, such as the starfish, affected the densities of others. His graphical depictions of intertidal FWs were thus dependent upon which species he selected to manipulate and what experiments he conducted. Perhaps because of his aversion to the crudity of trophic levels, his FWs illustrate a type of parsimony using mostly a few individual animal species and not functional groups although he did lump groups of plant species (algae, plankton, etc.) and groups of animals that were closely related taxonomically (species per genus, or genera per family), but were not identified to species. Because Paine was also more concerned with FW modules or compartments and quantitative abundance shifts, he did not say much about the canonical checkerboard pattern of TCs in his early studies.

If we imagine Figures 4 and 5 as having their bottom tiers fuelled by detritus instead of algae, this creates a 'parallel energy channel' (Ward et al., 2015). This interpretation then illustrates what Polis et al. (2000) termed the 'Apparent Trophic Cascade Hypothesis' (ATCH). It occurs when predators consume prey from a food chain based on detritus and not autotrophs. Ward et al. (2015) hypothesized if predators were advantaged by consuming detritus through a series of intermediate species in a detrital food chain, then their increasing numbers could force a TC down a grazing food chain. Pathway 4 in Figure 5 shows one way that this result could be produced, however, Pathway 1 also confirms that the opposite is true: nutrient enrichment can increase all variables in the top of the FW and then cause the top-down TC in the detritus food chain. This suggests that the use of the modifier 'apparent' should be reconsidered.

Paine (1980) defined the KP concept in 1969, as a species that when removed would cause "significant changes in population density, species composition, and overt appearance...[is] the keystone to the community structure and the integrity of the

community and its unaltered persistence through time". He also added that a KP need not be a major conduit for energy flow in the community. In the rocky intertidal zone, starfish preferentially consumed mussels, which was a superior space competitor when starfish were absent. Paine would simply throw the starfish into the ocean when he wanted to study the ecosystem without them. He essentially acted as a strong negative PI at the top of the FW like fishing a large predatory species to local extinction, and he also directly truncated the FW by eliminating the starfish variable and its links to its prey species. There were seven starfish-prey links in the Paine (1980) paper. Thus, even this single manipulation of starfish removal created massive changes in FW structure. In many FWs, it is not possible to dispose of an apex predator so conveniently. Clearly, he had deep insight into this ecosystem that was garnered from detailed observation and careful experimentation over many decades. Paine (1980) also understood that the FWs he studied changed seasonally, taxonomically, and geographically; this early result is often ignored in current FW studies when a single food web structure is used for a variety of locations and environmental conditions.

There have been other definitions of KP, for example, Menge et al. (1994) defined them as "only one of several predators in a community that alone determines most patterns of prey community structure, including distribution, abundance, composition, size, and diversity". Power et al. (1996) defined a keystone species "as one whose impact on its community or ecosystem is large and disproportionately large relative to its abundance". They summarized a great deal of information on KP observations and experiments over a range of ecosystems and analyzed the difficulties in field experimentation. They noted that many KPs, even *Pisaster ochraceus* studied by Paine, did not operate as a KP throughout its range, but rather there were various context-dependent factors that determined its role in any particular ecosystem.

Menge and his various collaborators, also working on the rocky intertidal zone in Washington State, provided FW models that are more consistent with loop models. For example, Menge and Sutherland (1976) compared two FWs representing exposed (15 species) versus protected (22 species) areas. There were two starfish species, *Pisaster* (larger predator) and *Leptasterias* (smaller predator), with two food chains beginning with detritus and plankton at the base with *Pisaster* on the top, and macro algae at the base with *Leptasterias* on the top like Figure 4. There was no direct interaction between the starfish species. Although there were more variables in these FWs than Figure 4, by transforming the links into a community matrix (not shown), several redundancies were found that would have lumped various combinations of species into fewer variables. Figure 5 illustrates a single KP, C_1^* . Undoubtedly, Figures 4 and 5 are oversimplified as representations of the rocky intertidal zone: for example, some studies have shown C_1 and C_2 consuming the same herbivore, and there is generally more omnivory occurring in the intertidal zone than depicted by Figures 4 and 5. Subsequent work has concluded that *Pisaster ochraceus* does not always function as a KP, but diffuse predation may be operating when many predators are present and their total effect may be strong, but not as individual species (Menge et al., 1994). In addition, there are many times when these ecosystems were driven from the bottom-up starting at the nutrient level (Menge, 1992). Some of the disparate results can also be related to how TCs are defined.

In Figures 4 and 5, it appeared that two parallel food chains could explain much of the community structure of the rocky intertidal zone that essentially resides on a two-dimensional plane with limited space, despite its curving downward into the ocean. Plankton communities, requiring three parallel food chains for minimum food web description, exist in a three-dimensional world where depth provides a great deal of habitat heterogeneity and opportunities for mixed survival strategies at different depths. A considerable evolutionary effort has gone into vertical migration and other adaptations across a wide variety of phyla to exploit the vertical axis in pelagic ecosystems. Briand and Cohen 1987 pointed out that when environments are three-dimensional or solid like a forest canopy or water column in the open ocean, they have distinctly longer food chains than environments that are two-dimensional. More work would have to be done in applying loop analysis to the rocky intertidal zone to determine if this observation has merit.

3.3 Definition of a Trophic Cascade

Polis et al. (2000) asked when is a trophic cascade (TC) a trophic cascade? TCs historically have not been easy to define, and at present, a universally-accepted definition or even a set of agreed-upon criteria for such a definition remains elusive. Often definitions include arbitrary components. The ‘arbitrary’ pervades the study of ecological systems not only in definitions, but also in conceptualization, methodology, modelling, statistical testing, and an array of other practical considerations. Every definition also involves embedded assumptions that have consequences. At a minimum, we should expect that a TC definition should be theoretically and conceptually coherent and realistic, be able to satisfy practical and logistical requirements such as being observable and measurable in the field and laboratory, and be overall useful in its applications.

Ripple et al. (2016) critically evaluated ten TC definitions in the literature (1994 to 2006) that are representative of the current conceptualization of this term; their work makes a convenient starting point for this section. They concluded that the term ‘trophic cascade’ has been in definitional limbo and “this has resulted in imprecise usage and thinking” and without better definitional clarity, the concept “risks falling into the realm of uselessness”. Finding previous definitions inadequate, these authors proposed their own definition: “trophic cascades are indirect species interactions that originate with predators and spread downward through FWs”. Clearly, a “foundation of modern ecology” requires a clear definitional and conceptual basis. Most of the definitions Ripple et al. (2016) reviewed are listed in Table S9 with their own definition as the last row of the table. Each one is analyzed through the lens of LA in the right-hand column, and found to be lacking.

Table 1 is divided into the theoretical and conceptual as well as practical considerations by systematically asking a set of questions about any potential TC definition. For example, what should the pattern of a TC be both theoretically and practically? The answer is the same: the canonical checkerboard pattern (Carpenter, et al., 1985) since the pattern needs to be both predictable and recognizable with field and laboratory FWs. Many species such as insects in terrestrial ecosystems and plankton in aquatic ecosystems are erratic in their abundance patterns over an annual cycle. Given the diversity of prediction patterns for Figures 1-5 for all PIs, the only patterns that are reasonably predictable are all zeros, all + signs or all – signs, and the checkerboard pattern. We need to recognize these patterns if we are to identify the potential locations of the dominant PIs, which is not a trivial undertaking. Regardless of how many variables exist on

the pathway from the first to the last variable, we know that once a three variable path is determined, we can predict the rest using this small subset of prediction patterns. Ripple et al.'s (2016) definition does not mention any particular pattern, but it does require all top to bottom pathways to end arbitrarily at the bottom of the FW and to include at least three variables.

Table 1. Components of and Considerations in Defining Trophic Cascades.

N = the total number of variables in the food web and $K < N$.

A. Theoretical & Conceptual Considerations	Loop Analysis Suggests:
1. What patterns are allowed?	The canonical checkerboard pattern going from the top to the bottom of the FW.
2. Which/how many variables are allowed?	At a minimum three: one at or near the top of the FW, and one at or near the bottom of the FW with one in-between and causally connected to the other two via direct predator-prey links.
3. Which/how many links are allowed?	At a minimum two, up to $N-1$ links as all predator-prey or consumer-resource links.
4. Which/how many PIs or drivers are allowed?	A minimum of one PI per trophic cascade, recognizing that a single FW may have more than one trophic cascade operating with one to a few PIs in total.
5. Which/how many pathways are allowed?	Can be one to a few operating pathways per trophic cascade with the same start and end variables.
6. What causality is allowed?	The requirements for a trophic cascade given above ensure that at a minimum there are two direct interactions and one indirect interaction among the three variables. At a maximum, there can be $K-1$ direct interactions for a pathway of K variables and $(K-2)!$ for each downward pathway
B. Practical Considerations	Loop Analysis Suggests:
1. What effects are allowed in variables?	Changes in standing crops of biotic variables and changes in concentrations of abiotic variables. Most commonly-used measures will be abundance, biomass, or weight. Rates of change of these measures should not be used (ex. productivity).
2. What effects are allowed in links?	Between each pair of variables included in a trophic cascade, there must be a predator-prey or resource relationship representing the direct links.
3. What effects are allowed in PIs?	PIs may be + or -.
4. What effects are allowed in pathways?	Only pathways with valid complements can constitute trophic cascades.
5. What patterns are allowed?	Only the canonical checkerboard pattern involving three or more variables.

Table 2 depicts the circumstances when these patterns are observable. The three elements on the left illustrate only bottom-up patterns and the three on the right show top-down patterns. To distinguish top-down from bottom-up patterns, the latter are termed ‘trophic escalades’ (TEs), which are defined below. Only the checkerboard pattern is unique for top-down pathway effects despite whether the PI starts at the top or near the top. The all-zero result regardless of beginning with a top or bottom variable requires a non-self-damped satellite variable attached to the variable receiving the PI or the pathway. This happens frequently in freshwater ecosystems when blue-green algae become abundant in the summer in the North Temperate Zone and they act as a satellite to the nutrient variable. They buffer it and it exhibits zero change. Likewise, all pathways through the nutrient to the rest of the FW or ending at the nutrient are zero since they do not have a valid complement. This network structure does not appear to occur in marine ecosystems, but this requires more study (Lane, 2016). Thus, only the checkerboard pattern remains observable and reliably predictable for top-down pathways as Paine (2010) pointed out that alternative level effects are a hallmark of TCs.

Table 2. Summary of the Possible Pathways Beginning or Travelling Through the Bottom or Top of the FW that Give Predictable Patterns. (Predictions are given here for three variables, but apply to any number ≥ 3 .)

	Pathway Enters Bottom Variable and Travels Upward (Bottom-Up Trophic Escalade)*	Pathway Enters Top Variable and Travels Downward (Top-Down Trophic Cascade)*
Attached to Satellite Variable	0 0 0	0 0 0
Not Attached to Satellite Variable & Top Variable Self-damped	+++ or ---	+ - + or - + -
Not Attached to Satellite Variable & Top Variable Not Self-damped	0 + 0 or 0 - 0 + 0 + or - 0 -	+ - + or - + -

A word of caution: to demonstrate a TC it is necessary, but not sufficient to document the checkerboard pattern, and also it is not sufficient to prove the PI begins at the top variable. For example, Heath et al. (2014) defined TCs as originating as a change in a top predator assuming it is motivated by the predator’s response to an external perturbation, but top predators can be impacted and change from pathways originating from any other part of the FW. For example, in Figure 5, the two food chain model connected by one top carnivore, produced several predictions of checkerboard patterns in both the top and bottom tiers of the FW (Table S7: Rows # 1, 2, 7, 9, 10, 11), that began low in the trophic hierarchy of one tier, travelled up, and then down the other tier. Thus, even the presence of a checkerboard pattern does not prove that the TC began at the top of the FW and it tells us nothing about the source of external perturbation (PI), which may not be ‘top-down’.

The human mind it is attracted to simple patterns, and the checkerboard pattern is one of the most recognizable of all in FWs. If we know the pathway of effect and a change in

any variable along that pathway, we can predict the changes in all variables as either plus or minus as well as their associated correlation patterns with LA. The definition of a TC based upon LA is:

A trophic cascade (TC) is all or part of an operating pathway, including at least three adjacent variables, starting with a variable at or near the top of the food web and ending with a variable at the bottom, with all the links on the pathway representing predator-prey and consumer-resource interactions that produce a checkerboard pattern (+ - + or - + -) of changes in the standing crop of the path variables.

A TC requires at least three predictions to determine if a checkerboard pattern exists; Paine (2010) also used this criterion. This three-variable pathway is composed of two direct effects and one indirect one. In addition, the pathway must be operating for there to be changes in the variables along the pathway. Since only a minimum of three variables is needed, the pathway does not have to start with a single apex predator. FW structures vary a lot; there may be more than one top predator, but there needs to be enough variables between the top and bottom to ensure the requirement of a minimum of three variables can be achieved. Fewer than three variables does not ensure a definitive checkerboard pattern since there would be only two variables with opposite sign. A TC beginning with an apex predator versus a meso-predator will differ in number of variables on the path (one less variable and one less link), but not in any ways that matter to the essence of a TC. Likewise, how the bottom of the FW is structured can vary, for example, whether nutrients are included or not. If not, the TC pathway may end at a primary producer variable, although as the bottom variable, it would always be self-damped (Levins, 1975).

A TC *a priori* is a cascade of 'trophic' interactions; similarly, Paine (2010) included two predator-prey pairs joined in a downward pathway in his definition. In LA, these are links that have a circle-head (-) on one end and an arrow head (+) on the other, which depict predator-prey or consumer-resource interactions, and the downward pathway travels from one variable to another through the circle-heads. Since the links are multiplied in LA as algebraic signs, this ensures an odd number of circle-head links will give a negative effect whereas an even number of circle-head links will produce a positive effect and thus, the overall checkerboard pattern. In some instances, an arrowhead may be missing at a particular time of year, for example, when luxury consumption is occurring between the phytoplankton and nutrient variables in a marine food web. This does not interfere with the identification of a TC and for most of an annual cycle the two-way link would be present. In addition, there can be multiple pathways moving down the FW beginning with a PI to a predator as in Figures 4 and 5, which can lead to different predictions (See rows labelled "Result" in the Community Effects Matrices in Tables S4 and S7). Thus, a TC arising from a single valid pathway could be dominated by other non-TC pathways and not be observable in nature.

The definition of a TC given here includes some inherent, but unavoidable arbitrary characteristics. For example, of the numerous pathways of effect that might be operating in a FW, we attach ecological importance to only one (to a few) that is visible at or near the top of the FW with either apex predators or meso-predators, and that essentially acts as a downward food chain(s). Our understanding and observations\measurements of TCs have been based on relatively simple ecosystems where food chains predominate. Thus, we

have been prisoners to our disciplinary history. There are many other pathways that can begin at or near the top and then travel laterally and/or even in zigzag patterns until reaching a bottom variable. These latter pathways do not have distinct or predictable patterns of change unless they are modelled accurately such as with data-fitted loop models (Lane, 2016). Thus, these pathways are not considered to be TCs (Paine, 2010). Likewise, there can be non-trophic links involved in various pathways of effect that I arbitrarily omit in the TC definition. Some authors have suggested that non-consumer links should be included; these links can take several qualitative forms in operating pathways and they are not infrequent (Schmitz et al., 2004). *A priori* they are non-trophic.

With this definition, like Ripple et al. (2016), I also arbitrarily cease my interest in the pathway when it reaches the lowest variable. There appears to be no ecological justification for this restriction ('stop at the bottom') other than a practical one of pattern recognition when a pathway turns upward. Ripple et al. (2016) termed additional pathway effects as 'knock-off effects' or 'spin offs'. These are also arbitrary terms. When the pathway moves past this lowest variable and turns upward, the checkerboard pattern will disintegrate since most upward pathways traverse through links with positive arrowheads and not negative circle-heads. There are, however, many other arbitrary aspects of FW studies that affect TC definitions. Winemiller and Layman (2005, p 13) pointed out: "The spatial and temporal boundaries of a community food web are always arbitrary, and it should be emphasized in any food web is the module or subnetwork embedded within the larger system... Spatial and taxonomic limits of modules are essentially arbitrary." Thus, the TC definition used here addresses many of the flaws in other definitions, but shares some similarities to many of them and in particular, agrees with Paine (2010) on the main points. Whereas my definition, like all others, is not devoid of arbitrary decisions, they are made as logically and transparently as possible with the bias toward field recognition and based upon achieving consistency with LA results and observations.

The predictions of all +'s or all -'s in the bottom left-hand square of Table 2 confirm that bottom-up pathways of effect can also be predictable in real world FWs. This is because these pathways travel largely through the arrowheads (+) from the bottom to the top of the FW. The only difference is whether the overall community effect is positive or negative at the initial variable of interest. If positive, then all variables increase going up the FW, and if negative, all variables decrease. These options arise either from sign change in: (1) a PI at the initial variable, or (2) in the pathway transiting through the initial variable from elsewhere in the food web.

If the bottom-up pathways had a different name than 'trophic cascade', which has become generally, but not universally, established as a top-down phenomenon, much confusion could be eliminated. Hunter and Price (1992) pointed out that 'cascading upwards' is an oxymoron. Whereas bottom-up pathways are composed of predator-prey links with a circle-head on one end and an arrowhead on the other, and recognizing that a cascade like those associated with waterfalls only cascade downwards, it would be useful to distinguish the two using a term like 'trophic escalade' (TE) for bottom-up trophic pathways and effects. The term originally meant "to climb up and over" a fortification or castle wall, but since 'escalade' essentially depicts an upward progression, it appears to capture the notion of bottom-up effects in a FW at least as well as a cascade depicts downward flow. Separate and distinct definitions are needed because top-down and

bottom-up terms have been overused and applied in so many diverse situations as to be almost meaningless. Thus, a precise TE definition that complements the one given here for TCs using a LA conceptual basis it is as follows:

A trophic escalate (TE) is all or part of an operating pathway, including at least three adjacent variables, starting with a variable at or near the bottom of the food web and ending with a variable at the top, with all the links on the pathway representing predator-prey and consumer-resource interactions that produce a uniform pattern of changes (+ + + or - - -) that can sometimes include zeros on alternative levels of the pathway.

Similar to TCs, a TE can involve multiple pathways moving up the FW beginning with a PI to a nutrient or primary producer as in Figures 4 and 5, which can lead to different predictions (See rows labelled “Result” in the Community Effects Matrices in Tables S4 and S7). Like TCs, a TE arising from a single valid pathway could be dominated by other non-TE pathways and not be observable in nature. The bottom-up pathway is also sensitive to whether the top variable is self-damped or not in contrast to a TC that always has a self-damped variable at the bottom. Without self-damping at the top, there are fewer valid complements resulting in alternating zeros in the prediction pattern, which is more difficult to recognize and predict in nature. The zeroes indicate increased or decreased turnover rates in those variables if adjacent variables above and below the variable of interest both increase or decrease together. Heath et al. (2014) termed the zeroes ‘skipped levels’ and suggested elaborate explanations such as weak consumer regulation or predominant trait-mediated uptake regulation. Actually the zeroes are quite straightforward, and it is not necessary to invoke these mechanisms.

Ripple et al.’s (2016) definition listed in Table S9 is itself imprecise and impractical if one objective is to be able to recognize TCs in nature. They include only indirect links, yet indirect links *a priori* arise from direct ones. This is a false dichotomy. For direct links, they include all trophic and non-trophic interactions. Trophic links are a key determinant of the checkerboard pattern since many non-trophic links cause lateral flows in the pathways (e.g. negative algal shading or toxicity, positive algal metabolite release, or immature zooplankton becoming adults) and do not always involve circle-heads negatively impacting the next lowest variable on the path. Ripple et al. (2016) included only downward pathways originating with predators and assumed all pathways are equally operational. They are not. *A priori*, non-operating pathways are not observable in nature and do not count as an outcome in an evolutionary sense. There can be numerous graphically-possible pathways that fit their definition, but many of these pathways would not have valid complements. Furthermore, it is impossible to determine valid complements from a species list and set of abundances data over time, that is, standard field data unless a tool like LA is used. Thus, there is no practical way to recognize TCs in the field using their definition. The authors also provide little guidance on how to distinguish downward trophic pathways from any lateral, zigzag, down-up-down, up-down-up, etc. pathways, which they exclude and which could blur the checkerboard pattern beyond recognition. Peterson et al. (2014) referencing McCann (2011), concluded that: “conceptualizing a TC as any indirect ecological effect of a predator is extremely permissive because most species in a FW are thought to be indirectly connected (if only weakly) to most other species of the FW... Whether a TC has occurred depends upon its definition”. Essentially, Ripple et al.’s

(2016) inclusion of all downward pathways is equivalent to LA calculations for the prediction row of the Community Effects Matrix for all valid pathways with any pattern of possible changes in standing crops for each variable impacted by a PI and with no constraint on the link type (trophic and non-trophic).

Ripple et al. (2016) also state that the only way to identify a TC is by experimentation, that is adding or removing predators to a FW, but many predators cannot be manipulated *in situ* and even in some of the best simulated marine mesocosms, such as MERL, even invertebrate predators do not survive well (Lane, 2016, In Press). In most marine micro- and mesocosm experiments, it has also proven impossible to replicate initial conditions across controls and treatments despite how meticulously they are established. Even in ecosystems amenable to experimental manipulations, logistical difficulties and sources of error are pervasive. Thus, requiring experimentation to identify TCs is impractical and often impossible. The authors also give no guidance on what type of pattern one should expect in a TC so that measurement can be targeted. I do not know of any experimental way, using abundance data, to recognize all operating paths from a predator to any other variable without using LA. The authors also give no guidance on when a PI might begin with a predator and how to distinguish a PI at the top of the FW versus the bottom since we know that experimentally manipulated PIs are not always the dominant ones in an experimental FW (Lane, 2016). Thus, with Ripple et al.'s (2016) definition and empirical requirements, there is also no way to identify a prediction pattern or its corresponding PI, and their definition is inadequate based upon the criterion of practicality.

Ripple et al (2016) are correct, however, in advocating for a better TC definition and improved field measurements. Better conceptualization is even more urgently needed than mere definition. Their definition agrees with the one used here in that it requires at least three variables, stresses downward pathways originating with predators, and arbitrarily ends at the bottom of the FW. The latter condition is necessary to ensure the checkerboard pattern is as clear as possible, although they do not use this reasoning. In summary, their definition is mostly at odds with the definition inspired by LA above and it would be helpful if Ripple et al. (2016) would clarify when and why their definition includes arbitrary components, some of which appear unnecessary and confusing.

3.4 Identifying Trophic Cascades

Nowhere does practicality matter more than in attempting to determine the existence and role of TCs in nature. TCs have been notoriously difficult to identify unequivocally in natural ecosystems (Heath et al. 2014); the difficulties are both theoretical/conceptual as well as practical. For aquatic systems, Polis and Strong (1996) concluded that "TCs are generally uncommon, except under a set of restrictive conditions that occur in some aquatic systems". Most success has come in low biodiversity environments in which the food web is simplified and approaching a food chain configuration. Often these environments are coastal and semi-enclosed with the long residence times, as compared to the more open pelagic zone. It is clear from comparing Figures 1 to 5 above that TCs are more obvious, less ambiguous, and more frequent in food chains than food webs. Ripple et al. (2016) concluded: "the consequences of a TC can only be seen and measured when the controlling predator is perturbed" [experimental approach]. These authors suggested the experiment could include adding or subtracting

predators, and studying either a time series or letting space substitute for time in a type of ergodic approach. This approach is not possible in all ecosystems, and even when possible, often does not provide a definitive test as the LA results above demonstrate.

Finding a TC also depends on how the investigator defines the term with its associated criteria. The definition of TC used here has been purposely designed to enhance the possibility of distinguishing a TC in the field as a checkerboard pattern (Table 2), however, the only way to do this was to introduce some arbitrary criteria, for example, considering only downward with a minimum of three variables that end at the bottom of the food web. In nature, pathways are oblivious to up-and-down. Furthermore, food webs do not come with labels nor can investigators interrogate their components: what is your functional group? Who did you eat today and who is likely to eat you? Are you being impacted by a PI, etc.? The investigator must decide how to conceptualize a set of imperfect species categories into functional groups and then measure the abundances of these biotic variables as well as concentrations of abiotic components. Investigators then use these patterns of standing crop changes to discern where the PI enters the food web and the resultant causal pathways it initiates sometimes not appreciating how complicated FWs can be. Despite the clarity of the 'checkerboard pattern', the PI causing it must dominate all others for a substantial time for a TC to be observable in nature. Even in this case, however, which levels increase and which decrease is a function of how many levels there are and how they are configured, that is, the structure of the whole system plus whether the dominant PI is + or -. How change is defined is often a highly arbitrary procedure, for example, is 10%, 20%, 50%, or more change in the standing crop of the variable necessary to distinguish a change from background variability?

With loop analysis, each row of the community effects matrix gives the predictions for the whole food web for all positive and negative PIs to each variable – not just those at the top or bottom. In addition, LA does not distinguish a top-down or bottom-up pathway as being more important than others and all pathways are included in calculating the changes in standing crops. If we consider the individual pathways (#1-#28) in Table S7 giving the 37 rows (28 individual variables and 9 result summaries) of predictions for Figure 5, there are 37 possible correlation patterns even for this relatively simple food web. These results also illustrate how a small structural change in a food web can have large effects on changes in standing crops as well as their correlation patterns. Many of these structural changes can be transient in nature, making the identification problematic, if not impossible, in the field. The multitude of potential correlation patterns illustrated in Tables S6 and S8 should serve as a warning. As food webs increase in complication, there can be a bewildering array of prediction patterns. Some authors attempt to document a TC in nature by one or two relationships from a possible set of $N^2-N/2$ correlation coefficients and have neither a biologically-reasonable, data-based food web nor an understanding of the dominant PI and its entry point into the food web. At best, this is a hit and miss procedure with a poor success rate.

Interestingly, if we compare the changes in standing crops for a PI to either predator C1* or C2* in Figure 4/Table S4, there is the classical checkerboard pattern going down the food web in tier 1 and tier 2 respectively, but when the pathway changes to the other tier and goes up the food web, all changes are positive indicating a TE. Thus, in a two-food chain food web that is devoid of lateral links, and which contains specialist predator-

prey pairs with connected predation at the top (Figure 5), if one food chain or tier is affected by a top predator, then the other simultaneously exhibits a bottom-up set of effects consistent with nutrient enrichment and a TE. In Figure 5/Table S7, there is only one KP and the checkerboard pattern is clearer for pathways #25 and #26, but not for #27 and 28. These results again serve as a warning that using only a few correlation coefficients to prove the existence of the TC in a complex ecosystem without knowing the others can be problematic. The total set of correlation patterns should be understood with a realistic food web model and accurate data set that are consistent before delineating a TC or TE and determining its role and in its FW.

There are other difficulties. First, LA tells us that every operating pathway must have a valid complement. Many pathways do not have valid complements. This implies that even though the potential for a TC mathematically exists in a food web, it may not be operating at a given date or even throughout the annual cycle. Second, field data in the form of a species list with abundance values is inadequate to distinguish operating from non-operating pathways or TCs from TEs. Third, the size and the duration of the effect in both TCs and TEs are left unspecified in most definitions as well as in many field and laboratory studies. Fourth, to attempt to identify a TC without a satisfactory model and only by one or two changes in standing crops of potential predator-prey or consumer-resource pairs is unreliable, yet it occurs frequently in the literature. Fifth, it should not be assumed that the PI can only originate in a TC at the top carnivore level. If carnivores are present in low abundance or only weakly interacting with the herbivores, the top-down TC pattern could originate at e.g. the herbivore level as in Pls 5A and B for Figure 1, 5B for Figure 2, and 3A and B for Figure 3, or even lower (Figures 4 and 5. This middle-up or middle-down pattern is not frequently identified in field data sets, but it most certainly occurs especially as one progresses from considering simple food chains to more complicated food webs. Sixth, some authors have suggested that since bottom-up TEs occur most often, they should also be considered, however, they only give a pattern of either all increases or all decreases in the food chain variables if the top trophic level is self-damped as in the Figures 1B and 2B (Table 2). If there is no self-damping at the top, then zero values in standing crops alternate levels of the pathway if there is beginning with the 0 at the lowest level for a model with an even number of trophic levels and a sign (+ or -) for an odd number of trophic levels. This type of pattern is more difficult to discern in nature than the checkerboard pattern, but not impossible. Most other sets of standing crop changes often appear random.

4.0 Conclusions

The Trophic Cascade Concept has been a dominant, if not an exalted, theme in ecology for several decades. This paper has contrasted several TC definitions and concepts using the lens of LA and Levins' caveat that "the truth is the whole". Food web representations and tools have varied greatly. To date, all models and approaches have been flawed, but unevenly so. While investigators always select what they consider most important and convenient to study, with TCs, it has too often been a single causal pathway or food chain, which it is considered propitious because its checkerboard pattern of effects is easiest to distinguish. Reductionist convenience, however, often comes with a cost in understanding. While every tool provides new information, it can also provide error and artifact. Even with LA, we can only look through the glass darkly given the levels of complexity and complication that are associated with ecosystems (Lane, 2016; In Press).

It is not unreasonable to ask why ecologists have attached so much significance to TCs over several decades. Has this level of attention been warranted? I think not, but finding patterns is a major goal in a new science. Originally, the notion of identifying the checkerboard pattern and top-down driving forces (PIs) in nature was novel and exciting. Ecologists were mesmerized by the potential to discern indirect effects in the field and did not sufficiently appreciate how pervasive they are in all ecosystems. One can imagine the elation the young inquisitive Robert Paine felt in the 1960s as he began to tease apart the impact of his inscrutable starfish predator upon other species in the rocky intertidal zone. Also exhilarating, no doubt, was his ability to 'control' starfish densities through the simple act of tossing them into the sea. An area of science, like a person, however, eventually matures. Today, ecology is no longer 'new' and does not have the luxury of only documenting patterns or isolated mechanisms. Ensuring the persistence of a habitable planet rich in biodiversity requires ecology to mature, and for ecologists to employ more holistic thinking.

The simple food chains and webs in Figures 1 – 5 illustrate that TCs viewed in the context of the whole are not exceptional operating pathways, but a function of the structure of the whole FW. Even embedded in a complicated food web, a TC is not more ecologically-important than any other pathway that might start at or near the top or pass through the top of the FW, and travel to variables at the bottom of the FW. TCs represent one to a few causal pathways that can operate in FWs out of many hundreds of others. There can be no ecological rule that TCs and TEs are more important than other pathways, and indeed, pathways share variables and links so that it is difficult to isolate a single pathway of interest. Thus, a TC is not the "Holy Grail" of ecology (Terbough and Estes, 2010), and will not provide the predictive capacity that we require for ecosystem management.

John Gribbin (2004) seemed to understand this when he said: "in science, a complex system is one that is chaotic and in which way the system develops, feeds back on itself to change the way it is developing... The whole system has an important influence on every component and every component has an important influence on the host system. There are no components that sit around and essentially do nothing." For example, in LA, the configuration of the variables not on a pathway determines whether it will operate or not. These variables are in constant motion and not static insignificant isolates detached from their FWs. Nevertheless, investigators will continue to identify TCs in nature, but they will be largely ephemeral and subsumed within the whole networked set of operating pathways. Pathways in an N-variable FW can be any length up to N-variables long, thus, identifying a ≥ 3 variable checkerboard pattern can be commonplace as N increases. Analysing the total pattern of changes caused by each variable on all others is ultimately more useful via LA than focusing upon identifying one to a few causal pathways of ≥ 3 variables.

If LA modelling was undertaken for more ecosystems to create data-fitted loop models, however, we might understand food webs and TCs/TEs more accurately and with an improved perspective. At a minimum, LA provides a calculation of the totality of simultaneously-operating feedbacks in a whole food web. By selecting only a TC in a food chain or small food web, however, this severely constrains the results as well as their significance. Furthermore, the TC definition used in this paper also reduces that

significance, but hopefully making it more realistic and practical. There is also an urgent imperative to improve our perspective. Should we be spending so much of our effort on a few causal pathways like TCs and TEs, when our fate depends upon all causal pathways? We simply cannot escape “the truth is the whole”.

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A Review of the Trophic Cascade Concept Using the Lens of Loop Analysis: the Truth Is the Whole by Patricia A. Lane

Supplementary Tables

Table S1. Community Effects Predictions and Correlation Patterns for Figure 1.

No.	Parameter Input (PI)	N_1	A_1	H_1	Correlation Patterns
1A	$+N_1$	+	0	+	N_1 and H_1 are positively correlated, but neither is correlated with A_1 .
1B	$+N_1$	+	+	+	All variables are positively correlated.
2A	$-N_1$	-	0	-	N_1 and H_1 are positively correlated, but neither is correlated with A_1 .
2B	$-N_1$	-	-	-	All variables are positively correlated.
3A	$+A_1$	-	0	+	N_1 and H_1 are negatively correlated, but neither is correlated with A_1 .
3B	$+A_1$	-	+	+	N_1 is negatively correlated with A_1 and H_1 whereas A_1 are positively correlated with each other.
4A	$-A_1$	+	0	-	N_1 and H_1 are negatively correlated, but neither is correlated with A_1 .
4B	$-A_1$	+	-	-	N_1 is negatively correlated with A_1 and H_1 whereas A_1 are positively correlated with each other.
5A	$+H_1$	+	-	+	Adjacent trophic levels are negatively correlated with each other whereas non-adjacent trophic levels are positively correlated with each other.
5B	$+H_1$	+	-	+	Adjacent trophic levels are negatively correlated with each other whereas non-adjacent trophic levels are positively correlated with each other.
6A	$-H_1$	-	+	-	Adjacent trophic levels are negatively correlated with each other whereas non-adjacent trophic levels are positively correlated with each other.
6B	$-H_1$	-	+	-	Adjacent trophic levels are negatively correlated with each other whereas non-adjacent trophic levels are positively correlated with each other.

Table S2. Community Effects Predictions and Correlation Patterns for Figure 2.

No.	Parameter Input (PI)	N_1	A_1	H_1	C_1	Correlation Patterns
1A	$+N_1$	0	+	0	+	A_1 and C_1 are positively correlated, but all other correlations are zero.
1B	$+N_1$	+	+	+	+	All variables are positively correlated.
2A	$-N_1$	0	-	0	-	A_1 and C_1 are positively correlated, but all other correlations are zero.
2B	$-N_1$	-	-	-	-	All variables are positively correlated.
3A	$+A_1$	-	+	0	+	N_1 is negatively correlated with A_1 and C_1 which are positively correlated with each other. H_1 is not correlated with the other variables.
3B	$+A_1$	-	+	+	+	N_1 is negatively correlated with A_1 , H_1 , and C_1 , which are all positively correlated among themselves.
4A	$-A_1$	+	-	0	-	N_1 is negatively correlated A_1 and C_1 which are positively correlated with each other. H_1 is not correlated with the other variables.
4B	$-A_1$	+	-	-	-	N_1 is negatively correlated with A_1 , H_1 , and C_1 which are all positively correlated among themselves.
5A	$+H_1$	0	0	0	+	There are no correlations.
5B	$+H_1$	+	-	+	+	N_1 , H_1 , and C_1 are positively correlated among themselves and negatively correlated with A_1 .
6A	$-H_1$	0	0	0	-	There are no correlations.
6B	$-H_1$	-	+	-	-	N_1 , H_1 , and C_1 are positively correlated among themselves and negatively correlated with A_1 .
7A	$+C_1$	-	+	-	+	Adjacent trophic levels are negatively correlated with each other whereas non-adjacent trophic levels are positively correlated with each other.
7B	$+C_1$	-	+	-	+	
8A	$-C_1$	+	-	+	-	Adjacent trophic levels are negatively correlated with each other whereas non-adjacent trophic levels are positively correlated with each other.
8B	$-C_1$	+	-	+	-	

Table S3. Community Effects Predictions and Correlation Patterns for Figure 3.

No.	Parameter Input (PI)	N_1	A_1	H_1	C_1	C_1^*	Correlation Patterns
1A	+ N_1	+	0	+	0	+	A_1 , H_1 , and C_1^* are positively correlated with each other, but all other correlations are zero.
1B	+ N_1	+	+	+	+	+	All variables are positively correlated.
2A	+ A_1	0	0	+	0	+	H_1 and C_1^* positively correlated with each other and there are no other correlations.
2B	+ A_1	-	+	+	+	+	A_1 , H_1 , C_1 , and C_1^* are all positively correlated among themselves, and all are negatively correlated with N_1 .
3A	+ H_1	+	-	+	0	+	N_1 , H_1 , and C_1 are all positively correlated among themselves, and all are negatively correlated with A_1 . C_1 has no correlations with other variables.
3B	+ H_1	+	-	+	+	+	N_1 , H_1 , C_1 , and C_1^* are all positively correlated among themselves, and all are negatively correlated with A_1 .
4A	+ C_1	0	0	0	0	+	There are no correlations between any pair of variables.
4B	+ C_1	-	+	-	+	+	A_1 , C_1 , and C_1^* are all positively correlated among themselves, and all are negatively correlated with N_1 and H_1 , which are positively correlated with each other.
5A	+ C_1^*	+	-	+	-	+	This is the classic top-down pattern of alternating signs, with adjacent trophic levels negatively correlated with each other
5B	+ C_1^*	+	-	+	-	+	

Table S4. Community Effects Predictions for Figure 4.

PI	Sets of Paths	N ₁	A ₁	H ₁	C ₁	C ₁ *	N ₂	A ₂	H ₂	C ₂	C ₂ *
+N ₁	#1	+	+	+	+	+	-	+	+	+	+
	#2	+	+	+	+	+	-	+	+	+	+
	#3	+	+	+	+	+	-	-	-	-	-
	Result	+	+	+	+	+	-	?	?	?	?
+N ₂	#4	-	-	-	-	-	+	+	+	+	+
+A ₁	#5	-	+	+	+	+	-	-	-	-	-
	#6	-	+	+	+	+	+	-	-	-	-
	#7	-	+	+	+	+	-	-	-	-	-
	#8	+	+	+	+	+	-	-	-	-	-
	Result	?	+	+	+	+	?	-	-	-	-

+A ₂	#9	-	-	-	-	-	-	+	+	+	+
	#10	-	-	-	-	-	+	+	+	+	+
	Result	-	-	-	-	-	?	+	+	+	+
+H ₁	#11	+	-	+	+	+	-	+	+	+	+
	#12	-	-	+	+	+	+	+	+	+	+
	#13	+	-	+	+	+	+	+	+	+	+
	Result	?	-	+	+	+	?	+	+	+	+
+H ₂	#14	+	+	+	+	+	+	-	+	+	+
	#15	+	+	+	+	+	-	-	+	+	+
	Result	+	+	+	+	+	?	-	+	+	+
+C ₁	#16	-	+	-	+	+	+	-	-	-	-

PI	Sets of Paths	N ₁	A ₁	H ₁	C ₁	C ₁ *	N ₂	A ₂	H ₂	C ₂	C ₂ *
	#17	+	+	-	+	+	-	-	-	-	-
	#18	+	+	-	+	+	-	-	-	-	-
	Result	?	+	-	+	+	?	-	-	-	-
+C ₂	#19	-	-	-	-	-	-	+	-	+	+
	#20	-	-	-	-	-	+	+	-	+	+
	Result	-	-	-	-	-	?	+	-	+	+
+C ₁ *	#21	+	-	+	-	+	-	+	+	+	+
	#22	-	-	+	-	+	+	+	+	+	+
	#23	+	-	+	-	+	-	+	+	+	+
	Result	?	-	+	-	+	?	+	+	+	+
+C ₂ *	#24	+	+	+	+	+	+	-	+	-	+
	#25	+	+	+	+	+	-	-	+	-	+
	Result	+	+	+	+	+	?	-	+	-	+

Table S5. Selected Sets of the Longest Operating Paths (indirect Effects) by Number of Parameter Input Given in Table S4 for Figure 4.

1. N_1 to A_1 to H_1 to C_1 to C_1^* and N_1 to A_2 to H_2 to C_2 to C_2^* and N_1 to A_1 to N_2
2. N_1 to A_1 to H_1 to C_1 to C_1^* and N_1 to A_2 to H_2 to C_2 to C_2^* and N_1 to A_2 to N_2
3. N_1 to A_1 to H_1 to C_1 to C_1^* and N_1 to A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
4. N_2 to A_2 to N_1 to A_1 to H_1 to C_1 to C_1^* and N_2 to A_2 to H_2 to C_2 to C_2^*
5. A_1 to H_1 to C_1 to C_1^* and A_1 to N_1 to A_2 to H_2 to C_2 to C_2^* and A_1 to N_2
6. A_1 to H_1 to C_1 to C_1^* and A_1 to N_1 to A_2 to N_2 and A_1 to N_1 to A_2 to H_2 to C_2 to C_2^*
7. A_1 to H_1 to C_1 to C_1^* and A_1 to N_1 and A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
8. A_1 to H_1 to C_1 to C_1^* and A_1 to N_2 to A_2 to N_1 and A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
9. A_2 to N_1 to A_1 to H_1 to C_1 to C_1^* and A_2 to N_2 and A_2 to H_2 to C_2 to C_2^*
10. A_2 to N_1 to A_1 to H_1 to C_1 to C_1^* and A_2 to N_1 to A_1 to N_2 and A_2 to H_2 to C_2 to C_2^*
11. H_1 to C_1 to C_1^* and H_1 to A_1 to N_1 to A_2 to N_2 and H_1 to A_1 to N_1 to A_2 to H_2 to C_2 to C_2^*
12. H_1 to C_1 to C_1^* and H_1 to A_1 to N_1 and H_1 to A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
13. H_2 to C_2 to C_2^* and H_2 to A_2 to N_2 and H_2 to A_2 to N_1 to A_1 to H_1 to C_1 to C_1^*
14. H_2 to C_2 to C_2^* and H_2 to A_2 to N_1 to A_1 to N_2 and H_2 to A_2 to N_1 to A_1 to H_1 to C_1 to C_1^*
15. C_1 to C_1^* and C_1 to H_1 to A_1 to N_1 to A_2 to N_2 and C_1 to H_1 to A_1 to N_1 to A_2 to H_2 to C_2 to C_2^*
16. C_1 to C_1^* and C_1 to H_1 to A_1 to N_2 to A_2 to N_1 and C_1 to H_1 to A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
17. C_1 to C_1^* and C_1 to H_1 to A_1 to A_1 to N_1 and C_1 to H_1 to A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
18. C_2 to C_2^* and C_2 to H_2 to A_2 to N_2 and C_2 to H_2 to A_2 to N_1 to A_1 to H_1 to C_1 to C_1^*
19. C_2 to C_2^* and C_2 to H_2 to A_2 to N_1 to A_1 to N_2 and C_2 to H_2 to A_2 to N_1 to A_1 to H_1 to C_1 to C_1^*
20. C_1^* to C_1 to H_1 to A_1 to N_1 to A_2 to N_2 and C_1^* to C_1 to H_1 to A_1 to N_1 to A_2 to H_2 to C_2 to C_2^*
21. C_1^* to C_1 to H_1 to A_1 to N_2 to A_2 to N_1 and C_1^* to C_1 to H_1 to A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
22. C_1^* to C_1 to H_1 to A_1 to A_1 to N_1 and C_1^* to C_1 to H_1 to A_1 to N_2 to A_2 to H_2 to C_2 to C_2^*
23. C_2^* to C_2 to H_2 to A_2 to N_2 and C_2^* to C_2 to H_2 to A_2 to N_1 to A_1 to H_1 to C_1 to C_1^*
24. C_2^* to H_2 to A_2 to N_1 to A_1 to N_2 and C_2^* to C_2 to H_2 to A_2 to N_1 to A_1 to H_1 to C_1 to C_1^*

Table S6. Summary of Correlation Patterns by Parameter Input (PI) for Figure 4 and Tables S4 and S5. For those parameter inputs associated with multiple paths, the ‘Result’ row is described. Tier 1 is the top row of the model (variables with subscript 1) and tier 2 (variables with subscript 2) is the bottom row of the model.

PI	Path or Result (R)	Correlation Patterns
N₁	R (1-3)	All tier 1 variables are positively correlated among themselves and negatively correlated with N2. The rest of the tier 2 variables are ambiguous by pathways 1 and 2 they are all positive and by pathways 3 they are all negative.
N₂	4	All tier 1 variables are positively correlated with each other and similarly all tier 2 variables are positively correlated with each other while all tier 1 variables are negatively correlated with all tier 2 variables.
A₁	R (5-8)	Both nutrients N1 and N2 are ambiguous. All other tier 1 or 2 variables are positively correlated within a tier whereas variables are negatively correlated between tiers.
A₂	R (9-10)	Only variable and to his ambiguous. All tier 1 variables are positively correlated with each other and similarly all tier 2 variables are positively correlated with each other while all tier 1 variables are negatively correlated with all tier 2 variables except for N2.
H₁	R (11-13)	Variables N1 and N2 are ambiguous. All other variables are positively correlated with each other except for A1 which is negatively correlated with all other variables except the nutrients.
H₂	R (14-15)	All variables are positively correlated with each other except for N2 which is ambiguous and A2 which is negatively correlated with the rest of the variables excluding N2.
C₁	R (16-18)	N1 and N2 are ambiguous. H1 is negatively correlated with A1, C1, and C1*, which are positively correlated among themselves. H1 is positively correlated with A2, H2, C2, and C2*, which are positively correlated among themselves. The tier 1 variables except for N1 and H1 are negatively correlated with all tier 2 variables except for N2.
C₂	R (19-20)	Tier 1 variables are all positively correlated among themselves. N2 is ambiguous and H2 is negatively correlated with a A2, C2, C2*, which are positively correlated among themselves. The tier 1 variables are negatively correlated with A2, C2, and C2*.
C₁*	R (21-23)	The nutrients N1 and N2 are ambiguous. Except for N1, adjacent trophic levels in tier 1 are negatively correlated with each other whereas non-adjacent trophic levels in tier 1 are positively correlated – a top-down trophic cascade pattern. All non-nutrient variables in tier 2 are positively correlated with each other as well as positively correlated with H1 and C1* and negatively correlated with A1 and C1.
C₂*	R (24-25)	N2 is ambiguous. All tier 1 variables are positively correlated with each other. Except for N2, adjacent trophic levels in tier 2 are negatively correlated with each other whereas non-adjacent trophic levels in tier 2 are positively correlated – a top-down trophic cascade pattern.

Table S7. Community Effects Predictions for Figure 5.

PI	Sets of Paths	N ₁	A ₁	H ₁	C ₁	C ₁ *	N ₂	A ₂	H ₂	C ₂
+N ₁	#1	+	+	+	+	+	+	-	+	-
	#2	+	-	+	-	+	-	+	+	+
	#3	+	+	-	+	-	-	-	-	-
	Result	+	?	?	?	?	?	?	?	?
+N ₂	#4	+	-	+	-	+	+	+	+	+
	#5	-	-	-	-	-	+	+	-	+
	Result	?	-	?	-	?	+	+	?	+
+A ₁	#6	+	+	+	+	+	+	-	+	-
	#7	-	+	+	+	+	+	-	+	-
	#8	+	+	-	+	-	-	-	-	-
	#9	-	+	-	+	-	-	-	-	-
	Result	?	+	?	+	?	?	-	?	-
A ₂	#10	+	-	+	-	+	-	+	+	+
	#11	-	-	-	-	-	-	+	-	+
	Result	?	-	?	-	?	-	+	?	+
+H ₁	#12	+	-	+	+	+	+	-	+	-
	#13	+	+	+	+	+	+	-	+	-
	#14	-	-	+	-	+	+	+	+	+
	Result	?	?	+	?	+	+	?	+	?
+H ₂	#15	+	-	+	-	+	+	-	+	+
	#16	-	-	+	-	+	+	+	+	+
	#17	-	-	-	-	-	+	-	+	+
	Result	?	-	?	-	?	+	?	+	+
+C ₁	#18	-	+	-	+	+	+	-	+	-
	#19	-	+	-	+	-	+	-	-	-

	#20	+	+	+	+	+	+	-	+	-
	#21	+	+	+	+	+	-	-	+	-
	Result	?	+	?	+	?	?	-	?	-
+C₂	#22	+	-	+	-	+	-	+	-	+
	#23	+	-	+	-	+	-	+	+	+
	#24	-	-	-	-	-	-	+	-	+
	Result	?	-	?	-	?	-	+	?	+
+C₁*	#25	+	-	+	-	+	+	-	+	-
	#26	+	-	+	-	+	-	+	+	+
	#27	+	+	+	+	+	+	-	+	-
	#28	+	+	+	-	+	-	-	+	-
	Result	+	?	+	?	+	?	?	+	?

Table S8. Summary of Correlation Patterns by Parameter Input (PI) for Figure 5 and Table S7. For those parameter inputs associated with multiple paths, the 'Result' row is described. Tier 1 is the top row of the model (variables with subscript 1) and tier 2 (variables with subscript 2) is the bottom row of the model.

PI	Path or Result (R)	Correlation Patterns
+N ₁	R (1-3)	There were no correlations because of the high degree of ambiguity.
+N ₂	R (4-5)	A1 and C1 were positively correlated with each other and N2, A2, and C2 were positively correlated among themselves. These 2 groups of variables were negatively correlated with each other.
+A ₁	R (6-9)	A1 and C1 were positively correlated with each other and N2 and A2 were positively correlated with each other. These 2 groups of variables were negatively correlated with each other.
+A ₂	R (10-11)	A1, C1, and N2 were positively correlated with each other and A2 and C2 were positively correlated with each other. These 2 groups of variables were negatively correlated with each other.
+H ₁	R (12-14)	H1, C1*, N2, and H2, were all positively correlated with each other, but there were no other correlations due to ambiguity.
+H ₂	R (15-17)	A1 and C1 were positively correlated with each other and N2, H2, and C2 were positively correlated among themselves. These 2 groups of variables were negatively correlated with each other.
+C ₁	R (18-21)	A1 and C1 were positively correlated with each other and A2 and C2 were positively correlated with each other. These 2 groups of variables were negatively correlated with each other.
+C ₂	R (22-24)	A1, C1, and N2 were all positively correlated with each other, and negatively correlated with A2.
+C1*	R (25-28)	N1, H1, C1*, and H2 were all positively correlated with each other. There were no other correlations because of the high degree of ambiguity.

Table S9. Analysis of Ten Definitions of a Trophic Cascade Using Loop Analysis. Page references for the definitions in their original papers are given in Ripple et al. (2016).

A. Definition and Author	B. Critical Interpretation via Loop Analysis
"TCs are indirect effects mediated through consumer-resource interactions" (Wootton, 1994).	This definition is too general; it applies to the whole FW. All pathways exhibit indirect effects if they include more than two variables; indirect effects <i>a priori</i> arise from direct ones.
"The top-down (TC) model predicts that changes in the density of one trophic level are caused by the changes in the next higher trophic level and that such adverse correlations cascade down a FW". (McLaren and Peterson, 1994).	This definition is too restrictive for FWs; there can be more than one trophic cascade occurring simultaneously. Negative correlations do occur between adjacent trophic levels for downward pathways, but not two trophic levels with a third in-between them. They exhibit positive correlations. There is also the problem of delineating trophic levels in a FW in nature.
"The indirect interaction between predators and the resources consumed by the predator's prey" (Beckerman et al., 1997).	This definition is too general; it applies to the whole FW. While their example of an indirect interaction is correct, there can be many similar examples in a FW that are not part of a TC.
{T}Cs are defined as reciprocal predator-prey effects that alter the abundance, biomass or productivity of the population, community, or a trophic level across more than one link in a food chain" (Pace et al., 1999).	This definition is too general; it applies to the whole FW. Every operating pathway in a FW produces effects on all variables included within the pathway. The term 'reciprocal' also needs defining. Productivity is associated with turnover rates and it is different from the standing crops measurements of abundance and biomass.
"A TC is the progression of indirect effects by predators across successively lower trophic levels"(Estes et al., 2001).	A TC also includes direct effects. This definition suggests that every pathway going through a predator having an effect two links away is a TC. This definition is too general; it applies to much of the whole FW.
"TCs – the indirect effects of carnivores on plants mediated by herbivores" (Schmitz et al., 2004).	This definition suggests that for a TC to be a TC, it can begin with any carnivore, but must end with the primary producer. This definition is too restrictive and simultaneously too general since it encompasses all pathways from a carnivore to a plant variable. In Figure 1, a pathway originating with the herbivore could produce the canonical checkerboard pattern.
"Indirect positive affects of predators on plant biomass" (Borer et al., 2005).	Depending on the number of variables, a pathway through a predator travelling to a plant variable, could have + or - effect on the plant and still be in a TC.
The TC is the simplest top-down interaction: (i) predators suppress herbivores and allow plants to thrive, and (ii) apex predators suppress smaller meso- predators, releasing herbivores to suppress plants" (Strong and Frank, 2010).	Pathways in FWs can be any length up to and including the total set of N variables. The notion of 'simplest' it is not relevant to a TC. Their points (i) and (ii) are too restrictive and redundant. A single FW may contain a predator, apex predator, herbivore and plant in one food chain.
"A TC is the process by which a perturbation propagates either up or down the FW with alternating negative and positive effects at successive levels" (Terbough et al., 2006).	Operating pathways can be top-down or bottom-up, but bottom-up pathways cannot produce 'alternating negative and positive effects at successive levels'. This is incorrect. Depending on the PI to the bottom variable, the effects upwards will be all + or all - or alternating signs and zeros when the top variable is not self-damped. Except in the case where the bottom variable is linked to an un-damped satellite variable and then all effects upwards will be 0.
"TCs are indirect species interactions that originate with predators and spread downward through FWs" (Ripple et al., 2016).	<i>A priori</i> TCs include both direct and indirect effects. This definition is too general and imprecise. It also has several arbitrary features that are unnecessary; see Section 3.3.