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Trophic cascade direction and flow determine network flow stability

A.D. Canning*, R.G. Death

Institute of Agriculture and the Environment—Ecology, Massey University, Private Bag 11-222, Palmerston North, 4442, New Zealand

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ABSTRACT

The mechanisms for maintenance of food web structure and function in the face of frequent disturbance has been a question in ecology for many years. Local point-wise stability of theoretical food webs or robustness assessment of empirical binary food webs are the two principal techniques that have been used to address this question. However, many theoretical webs are often small, constructed randomly or from theoretical algorithms (such as Cascade or Niche models), and assume Lotka-Volterra dynamics. Whilst the binary webs used also assume all interactions are equal and that webs are donor controlled. Recent dynamic stability analysis of empirical quantitative webs has sought to improve this assessment. Here we investigate how aquatic food web structure and the direction of trophic cascades interact to affect the robustness of total carbon flow between species after a disturbance. The robustness of the 18 food webs is higher if predator control dominates. Webs with predator control were however stabilised by weak indirect interactions and short food chains.

1. Introduction

The complex nature of food webs (biological, directed networks of who eats whom within an ecosystem) makes it difficult to predict the cascading impacts of species loss following disturbance. However, with a growing global population, human impacts on ecological communities are increasing and the cascading impacts of these activities are difficult to predict and/or manage. Just one example of the many trophic cascades driven by anthropogenic disturbance is recorded by Ripple and Beschta (2006) who found increased visitors to Zion National Park, decreased cougar density that in turn increased Mule Deer density. The increased grazing of deer on cottonwoods increased soil erosion and reduced abundance and diversity of both terrestrial and aquatic taxa (Ripple and Beschta, 2006). This illustrates how disturbance can ripple through a web producing unforeseen outcomes. If it was possible to identify potential cascade pathways, then similar adverse chain reactions may be mitigated or avoided.

Although the influence of food web structure on stability has been extensively studied, it is still unclear exactly what the key parameters are for determining stability (Rooney and McCann, 2012; Saint-Béat et al., 2015). Here we consider stability to be a general term for the maintenance of food web structure and function over time, it includes various aspects such as equilibrium, persistence, resilience, robustness and resistance (Dunne et al., 2005). Complexity (i.e., aspects including diversity, connectance, pathway proliferation and link distribution) promote stability (by supporting predators with multiple energy pathways and dampening disruptive oscillations) or destabilize it by spreading disruptive oscillations (McCann, 2000; Rooney and McCann, 2012; Saint-Béat et al., 2015; Zhao et al., 2016). It is unclear whether long food chains (network paths) are always unstable or whether the stability is dependent on the underlying trophic dynamics in those food chains (Rooney and McCann, 2012; Saint-Béat et al., 2015). It is also unclear whether omnivory (feeding on multiple trophic levels) increases or reduces stability by suppressing or increasing oscillations (Gellner and McCann, 2012; Saint-Béat et al., 2015).

Much of the uncertainty around what drives stability arises because of differing methods for assessing stability, and/or differences in the implied trophic dynamics of the webs (McCann,

* Corresponding author.
E-mail address: a.d.canning@massey.ac.nz (A.D. Canning).

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2000). Early exploration by Gardner and Ashby (1970) and May (1972) showed that random large, well-connected food webs with Lotka-Volterra dynamics are unlikely to be stable. Whilst this was opposite to what Ecologists had hypothesized (MacArthur, 1955; Odum, 1969), it challenged Ecologists to understand what drives natural ecosystems to be stable. It was quickly identified that randomly generated webs with Lotka-Volterra dynamics are unrealistic assumptions for most food webs (Dunne et al., 2005); also, point-wise linear stability (i.e., eigenvalue analysis) may not reflect the stability of the entire food web (Ulanowicz, 1972). De Angelis (1975) used a similar modelling approach to May (1972); however, he showed that highly connected food webs could be stable if they had low assimilation efficiencies and a bias towards donor-control. More recently, McCann et al. (1998) showed, using theoretically generated food webs with empirically mimicked interaction strengths, Holling type III responses and non-equilibrium dynamics, that generalist-dominance and weak interactions stabilize webs by dampening oscillations. In addition, also primarily via theoretical studies, adaptive foraging with a mixture of strong and weak interactions (asymmetrical flows) are predicted to confer stability (Kondoh, 2003, 2006; Rooney et al., 2006; Uchida and Drossel, 2007). Adaptive foraging prevents cascading perturbations by allowing alternative energy supplies to establish should a link become perturbed. Consumers with both strong and weak interactions are able to feed on abundant species and exert recipient control; the less abundant species are consumed less allowing their populations to grow whilst the dominant competitor is kept in check (Rooney and McCann, 2012; Saint-Béat et al., 2015).

Despite these advancements in model food webs, whether these factors drive stability in empirically derived food webs has received much less attention. Most analysis of empirically derived webs has involved the assessment of topological robustness which involves simulating cascading extinction following initial species extinction (Dunne et al., 2002; Sole and Montoya, 2001). The advantage of this approach is that empirically derived food webs can be used, it indicates on whole-system responses, and a variety of perturbation events effects on whole web stability examined. However, to date this approach has mostly been applied to topological webs (interaction strengths are not quantified) (Dunne et al., 2005). They also assume webs are driven entirely by donor control dynamics (Dunne et al., 2002; Sole and Montoya, 2001). This methodology suggests that high connectance yields high robustness, and that highly skewed food webs are robust to poorly connected species but sensitive to the loss of well-connected species (Dunne et al., 2002; Gilbert, 2009; Ives and Cardinale, 2004; Sole and Montoya, 2001). Both eigenvalue analysis of theoretical webs and robustness of binary webs, therefore, have several limitations to their use and applicability in understanding and managing real ecosystems. Furthermore, Curtsdotter et al. (2011) showed that, in niche model generated webs, purely topological robustness tends to overstate robustness compared with dynamical robustness.

Dynamical robustness allows for the incorporation of indirect effects (via flow weighted food webs) and both predator control and donor control cascades, thus making them more realistic simulations. Recently, Zhao et al. (2016) applied dynamical robustness and found that food webs are most sensitive to secondary extinction when species are removed by their link weights rather than connectivity. Both diversity and connectance reduced robustness, in contrast to topological studies that found connectance increased robustness (Dunne et al., 2002; Zhao et al., 2016). They also found donor control cascades caused only half of the secondary extinctions, highlighting the importance for also assessing predator control along with donor control. Thereby highlighting the need for food web stability studies to move beyond theoretical models and empirically-derived topological webs to the assessment of flow-weighted food webs. With the increasing availability of well-defined flow-weighted food webs and ecological network analysis metrics (Borrett and Lau, 2014; Latham Ii, 2006), it is now possible to explore the drivers of dynamic robustness of empirically derived food webs. Greater analysis of empirical food web stability may also close the gap between theoretical constructs and conservation/management actions.

Ecosystem management is increasingly recognizing the importance of managing for ecosystem health in addition to traditional single species conservation approaches (Steedman, 1994). Healthy ecosystems are ones that maintain structure (organization) and function (vigor) over time in the face of disturbance (stability) (Costanza and Mageau, 1999). Structure or organization includes concepts such as species diversity, average mutual information and topological predictability. Whereas function or vigor includes concepts such as productivity, throughput, cycling, and flow based mutualism and synergism. Identifying stressors and understanding how they may distress the natural lifespan of an ecosystem's structure and function is, therefore, vital to the conservation of ecosystem health. To our knowledge, all studies of the stability of empirical webs have focused on the maintenance of organization (e.g., species richness) with few studies investigating the global stability of vigor – an equally vital component of ecosystem health (Mougi and Kondoh, 2016; Saint-Béat et al., 2015). Our study seeks to partially fill that gap by using 18 Carbon flow weighted foods to explore the structural and dynamic drivers of total Carbon through-flow stability (a measure of vigor) following random mass extinctions.

2. Material and methods

Eighteen aquatic food webs, spanning a range of diversity and complexity, with quantified carbon stores and flows were analyzed for their structure and dynamic robustness of carbon throughput (Table 1). The webs spanned a range of diversity and complexity, this is likely partly influenced by differing levels of resolution. However, the range of weighted webs publically available is small and we only chose webs that had more than 12 compartments to reduce the scaling constraints of small webs (Bersier and Sugihara, 1997).

The following network metrics of structure and carbon flow were calculated in R 3.0.3 (R Development Core Team, 2012) with packages NetIndices (Soetaert and Kones, 2008) and enaR (Borrett and Lau, 2014): the number of nodes, connectance (the per capita linkage density), Finn's Cycling Index (Finn, 1976), relative ascendency (Ulanowicz, 1997), the ratio of Indirect/Direct flows (inputs idealized) (Borrett et al., 2006; Fath and Patten, 1999; Latham Ii, 2006), the ratio of Indirect/Boundary flows, the Indirect Flow Intensity (Borrett et al., 2006), the average flow-based trophic level (Christensen and Pauly, 1993), and the average omnivory index (Christensen and Pauly, 1993).

Dynamic robustness, our indicator of stability, was defined as the percent of the original, pre-perturbed, web total system throughflow (the sum of all flows within a network) that occurred at a new steady state following the random loss of 25% of the nodes. The post-perturbation re-balancing followed the methods described by Allesina and Bondavalli (2003) and were carried out using the enaR (Borrett and Lau, 2014) package in R 3.0.3 (R Development Core Team, 2012). We chose a 25% extinction rate because in 2008 approximately one quarter of marine species assessed were listed in threatened categories (Critically Endangered, Endangered or Vulnerable) (Polidoro et al., 2008). Secondary species extinctions were not enumerated because it is unlikely that a compartment will be driven to zero completely in the model and there is insufficient data published on Allee Effects to estimate density dependent thresholds for each compartment; furthermore, the