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Review

Using food web dominator trees to catch secondary extinctions in action

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In ecosystems, a single extinction event can give rise to multiple ‘secondary’ extinctions. Conservation effort would benefit from tools that help forecast the consequences of species removal. One such tool is the dominator tree, a graph-theoretic algorithm that when applied to food webs unfolds their complex architecture, yielding a simpler topology made of linear pathways that are essential for energy delivery. Each species along these chains is responsible for passing energy to the taxa that follow it and, as such, it is indispensable for their survival. To assess the predictive potential of the dominator tree, we compare its predictions with the effects that followed the collapse of the capelin (*Mallotus villosus*) in the Barents Sea ecosystem. To this end, we first compiled a food web for this ecosystem, then we built the corresponding dominator tree and, finally, we observed whether model predictions matched the empirical observations. This analysis shows the potential and the drawbacks of the dominator trees as a tool for understanding the causes and consequences of extinctions in food webs.

Keywords: dominator tree; energy flow; food web; graph theory; secondary extinction

1. INTRODUCTION

The current biodiversity crisis has been framed in different ways. Concerns about species extinction projected into loss of ecosystem functions (i.e. soil fertility, climate regulation, pest control), reduced availability of food, medicines and genetic resources, and negative effects on human culture and its value system (Symstad *et al.* 1998; Chapin *et al.* 2000; Tilman 2000; Hooper *et al.* 2005).

Accordingly, searching for mechanisms that maintain biodiversity is of high interest for ecologists and biologists alike. In this framework, much effort has been devoted to understand how food-web structure (i.e. reciprocal dependence for food supply) affects extinction patterns (Borrvall *et al.* 2000; Dunne *et al.* 2002; Srinivasan *et al.* 2007).

Food webs are complex architectures depicting who eats whom in ecosystems. Their intricacy reveals that interdependence for food supply may extend across several trophic levels, connecting species that are far apart along the chain from producers to consumers. Owing to this extended dependence, a single extinction event may precipitate cascades of further extinctions (Greenwood 1987; Spencer *et al.* 1991), a phenomenon

that ecologists address as ‘secondary extinctions’. The multiplicity of connections may also buffer the consequences of food-web alterations as it may provide alternative routes for species to get their requisite medium when the main provider of food vanishes. To unveil the circumstances in which food-web structure amplifies or buffers the effects of species loss is of fundamental importance (Ripa *et al.* 1998).

Current research has focused on the level of connectivity in food webs, on the understanding that the more links one species establishes, the greater the damage to the community would be if that species were to go extinct (Dunne *et al.* 2002). However, connectedness (i.e. number of links) does not fully encompass the problem. In fact, it has been shown that no secondary extinction can be observed after removing the most connected species (through *in silico* experiments; Dunne *et al.* 2002; Allesina & Bodini 2004). Connectedness, in fact, is not synonymous with functional dependence or control; it accounts only for the number of links and not for their functional characteristics.

The key question is that of the real interdependence of species for food, which can be unveiled using dominator trees. This method comes from graph theory (Lengauer & Tarjan 1979; Aho *et al.* 1986) and has been recently applied to food webs (Allesina & Bodini 2004; Allesina *et al.* 2005) because it makes visible those pathways that are essential for energy delivery in food webs. Using the dominator tree, one can easily see which species act as bottlenecks for

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One contribution of 15 to a Theme Issue ‘Food-web assembly and collapse: mathematical models and implications for conservation’.

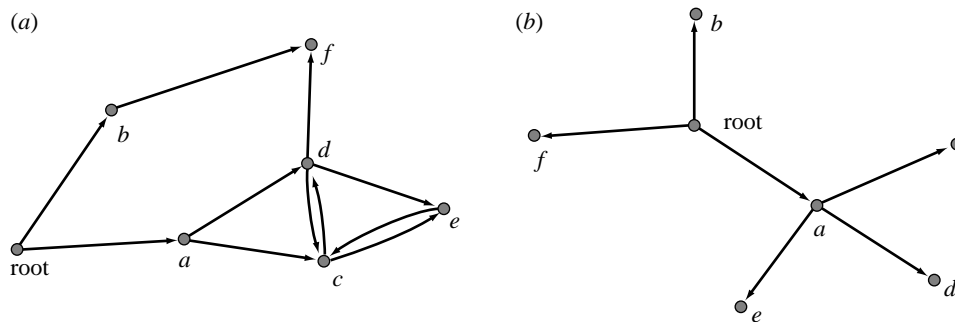


Figure 1. (a) Simple hypothetical food web and (b) its corresponding dominator tree. The removal of node *a* would cause the disconnection of nodes *c*, *d*, *e*, while the removal of any other node different from the root would cause no secondary extinction.

energy distribution to other species. Such bottlenecks are called dominators because their removal precludes energy from reaching the nodes that follow them in the chain from producers to consumers. By applying the dominator tree to a series of published food webs [Allesina & Bodini \(2004\)](#) showed how their intricacy could be unfolded to simpler structures that make apparent which nodes are likely to cause the greatest impact if removed.

The potential of the dominator tree to forecast secondary extinctions, however, must be validated to make this tool of practical utility, that is, in conservation science. The present paper addresses this question and presents the result of an investigation in which predictions of the dominator tree model were compared with observations of species disappearance following an extinction event. The case examined is that of the Barents Sea ecoregion, where the abundance of capelin (*Mallotus villosus*) collapsed twice, producing cascading consequences on sea birds and pinnipeds ([Hamre 1994](#); [Dolgov 2002](#)).

2. MATERIAL AND METHODS

(a) *The dominator tree*

Dominator trees are topological structures in which nodes are sequentially connected based on their dominance relations. [Figure 1](#) depicts, as an example, a simple food web and its dominator tree.

In both the food web and the dominator tree, *r* is a virtual node in which we collapse the external environment as the ultimate source of energy for the ecosystem. In food webs, domination is expressed in terms of energy delivery, and it can be said that node *x* is a dominator of node *y* if every path from *r* (root) to *y* contains *x*: that is to say, energy entering the system cannot reach *y* without visiting *x*. One of the fundamental theorems of dominator trees ([Lengauer & Tarjan 1979](#)) states that ‘every node of a graph except *r* has a unique immediate (i.e. closest) dominator’. Accordingly, we can build a dominator tree by connecting each node to its immediate dominator.

With reference to [figure 1](#), species *f* receives energy along the pathways $r \rightarrow a \rightarrow d \rightarrow f$ and $r \rightarrow b \rightarrow f$, but the dominator tree shows that only the root dominates *f*: it is the only node in common between the two paths. When either *a* or *d* become extinct, species *f* may survive because at least one pathway remains available. On the other hand, focusing on species *e* one perceives that all the energy available to it comes from the root and passes through *a*, so that both are dominators of *e*, and *a* is its immediate (closest) dominator.

We transformed the Barents Sea food web into a rooted network and we linked *r* to all basal species, nodes with no incoming links (autotrophs). This choice seems not only plausible, but also ecologically necessary. To survive, in fact, these nodes must receive energy from the external environment. For this food web, the dominator tree was constructed by computing the set of dominators for each node. This was done using an algorithm that selects iteratively common nodes between pathways ([Aho *et al.* 1986](#); [Allesina & Bodini 2004](#); [Allesina *et al.* 2005](#)). While we direct the reader to the cited bibliography for an accurate description of the algorithm; we provide here, in the electronic supplementary material A, a brief description that summarizes the procedure of calculation we used in this work.

3. RESULTS

(a) *The Barents food web*

The Barents food web has been reconstructed extracting information about species living in that ecoregion and their feeding habits from papers and reports (see [Larsen *et al.* 2001](#); [Dolgov 2002](#); [Ciannelli *et al.* 2005](#); [Stiansen *et al.* 2006](#) and references therein). It comprises 151 nodes (species and trophospecies) excluding the root node, and 1035 links. The food web is resolved at the species level except for phytoplankton, detritus and macro-algae, which appear as aggregated components (i.e. trophospecies). While the food web is depicted in [figure 2](#), in the electronic supplementary material B we provide a sketch of the Barents Sea ecosystem and the list of species comprised in the food web, together with their reference key numbers.

(b) *Secondary extinction in the Barents Sea*

The literature shows evidence that mechanisms potentially leading to secondary extinction were at work in the Barents Sea ([Hamre 1994](#); [Barret *et al.* 1997](#); [Barrett 2002](#); [Dolgov 2002](#); [Hjermann *et al.* 2004](#); [Ciannelli *et al.* 2005](#)). In two periods, 1984–1986 and 1992–1994, the large capelin fishery collapsed. This heavy reduction could potentially affect at least 21 fish species, 18 seabird species typical of the coastal and open Barents Sea, 3 pinniped species and 18 cetaceans, an evidence of the central role that capelin plays as a prey in this ecosystem.

Despite this large spectrum of predators, when the crisis became obvious in 1987, consequences were evident only in the abundance of the harp seal *Phoca groenlandica* and the common guillemot *Uria aalge*. The former species experienced mass migration, with hundreds of thousands individuals that invaded the

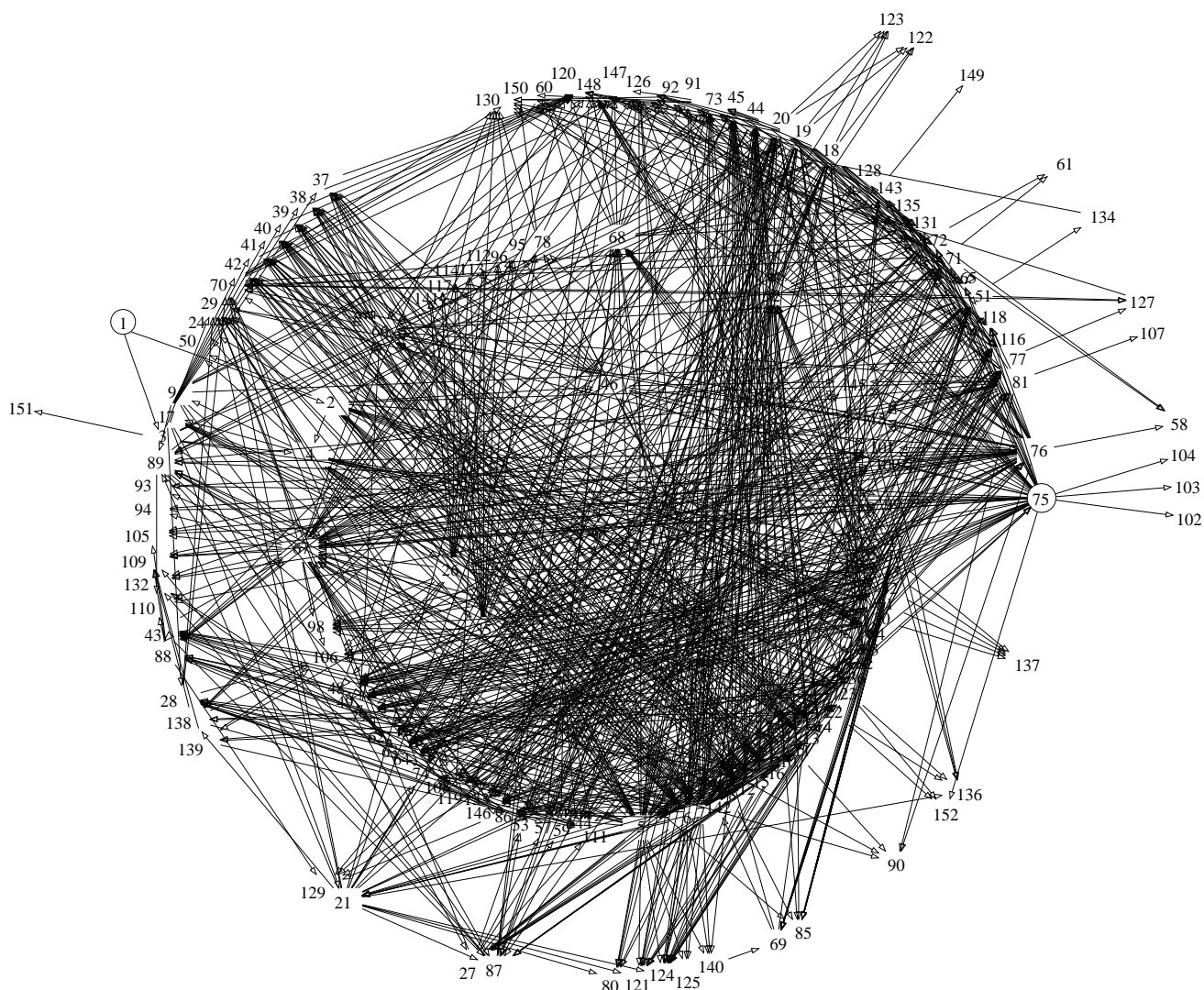


Figure 2. The food web of the Barents Sea ecoregion. The root (external environment) is labelled as node 1. Capelin is labelled as node 75. Electronic supplementary material B provides the correspondence between the other species and numbers in the food-web graph.

Norwegian coastal water; the common guillemot population collapsed by 70–90%. Based on this evidence, one can conclude that these species eventually would go locally extinct if the capelin collapse was complete.

(c) Dominator tree predictions

Unfolding the food web of this ecosystem yielded the graph of figure 3, which clarifies dominance relations between the nodes.

Most of the nodes in the food web are dominated by the root. This means that there are multiple pathways through which they gather their requisite resources and the only node necessary for their survival is the external environment as the ultimate source of energy. The capelin is node 75. It has phytoplankton (node 2) as its immediate dominator. Interestingly, this species is not an herbivore, and feeds on as many as 13 zooplankton species. Of these, none is a proper dominator of capelin and any single extinction of one of these species would have no (lethal) repercussion on capelin because in terms of the presence/absence of pathways there will be opportunities for capelin to feed on other zooplankton species. Phytoplankton becomes the

immediate dominator of the capelin, an obvious consequence of the fact that all algal species are aggregated in a single node. Capelin dominates three species: the kittiwake (node 102, *Rissa tridactyla*) the common guillemot (node 103, *U. aalge*) and the Brunnich's guillemot (node 104, *Uria lomvia*).

As many as 21 fish species, 18 seabirds plus 7 pinnipeds and some cetacean species prey on capelin. Of these, only three are dominated by this species; most of them rely on a large spectrum of resources and therefore capelin removal would not drive them extinct. This expectation is confirmed by observation, as in the Barents Sea the capelin collapse did not produce a significant reduction in the stock of most of its predators.

However, considering the species for which the dominator tree predicts fatal consequences following capelin removal, only the common guillemot (*U. aalge* node 102) confirmed this expectation: its abundance dropped by 70–90%. Moreover, the dominator tree does not predict the extinction of the harp seal (node 143, *P. groenlandica*), which, on the contrary, suffered greatly from capelin reduction. Finally, the cod (node 66, *Gadus morhua*) is not dominated by capelin. This means that,

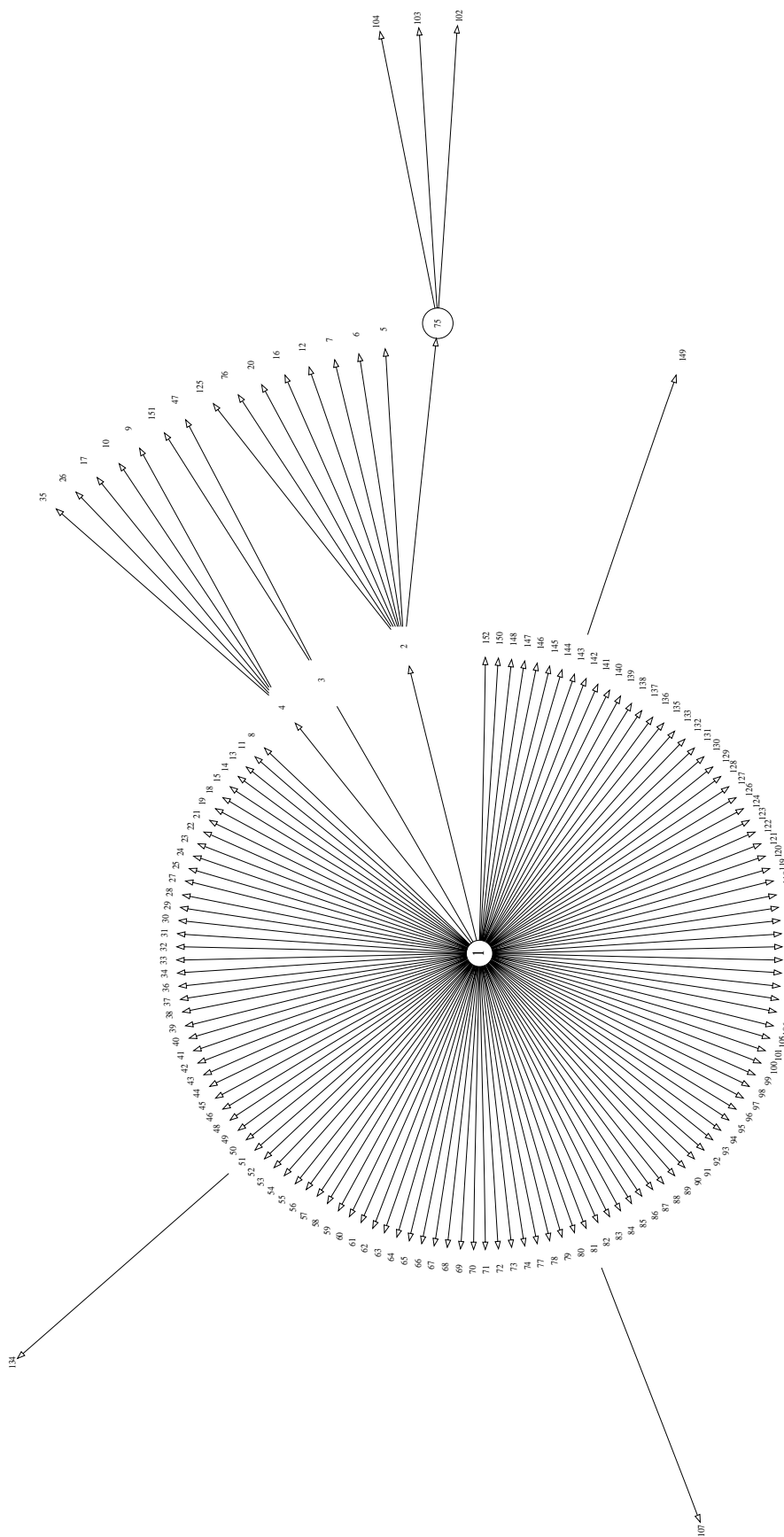


Figure 3. Dominator tree for the Barents Sea ecosystem. The capelin (node 75) dominates over *Rissa tridactyla* (102), *U. adge* (103) and *Uria lomvia* (104).

according to the dominator tree, no consequences would be expected for this species. What occurred in the ecosystem following capelin collapse confirms what the model predicts for cod: although capelin enters its diet in large proportion (37%), cod stock did not decrease dramatically, although there were effects on growth and maturation of individuals. Both these results can be explained by switching to less nutritious organisms (i.e. krill and amphipods).

4. DISCUSSION

Since it was shown that topological properties of networks determine their robustness with respect to node (species) removal (Albert *et al.* 2000), food webs, as paradigmatic examples of ecological networks, represented an ideal target for studying secondary extinction (Solé & Montoya 2001; Dunne *et al.* 2002, 2004; Memmott *et al.* 2004; Montoya *et al.* 2006; Srinivasan *et al.* 2007). In this framework, the dominator tree model (Allesina & Bodini 2004; Allesina *et al.* 2005) provides an elegant way to understand and predict which species are essential for the survival of others. It does this by unfolding food-web structures into linear pathways that are essential for energy delivery.

In this paper, dominator tree predictions for the Barents Sea food web are compared with *in situ* observations. They revealed the cascading effect of capelin stock collapse on the abundance of some predators, namely the common guillemot and the harp seal. Technically, capelin collapse is not a true extinction event, but the 95 per cent reduction in stock in the period 1984–1986 can be considered severe enough to induce in its predators the same response, at least qualitatively, than would be observed in case of complete collapse (local extinction). That is to say, what was observed is an intermediate condition for the system that would eventually be brought to a completion if capelin population vanished completely.

The main predator of capelin is the Atlantic cod. This species experienced some biomass reduction but did not collapse because it switched to less nutritious food such as crustaceans (krill and amphipods) and herring (Ciannelli *et al.* 2005). Prey switching is a mechanism that is not detected by the dominator tree (Allesina & Bodini 2004); accordingly, the dominator tree should include cod in the capelin branch. In this case, however, diet information available in literature included zooplankton and herring as potential prey for cod, and this yielded multiple predator–prey pathways involving cod in the food web. This extended multi-channel diet freed this species from capelin domination.

The harp seal is an interesting case. It underwent mass emigration in response to capelin reduction and this can be seen as an escape from collapse. For this exercise, however, emigration is equivalent to local extinction. The dominator tree does not show capelin dominating harp seal, and this would exclude fatal consequences for this latter species if the former is removed from the food web. To explain this incongruence between prediction and observation it is necessary to consider that the dominator tree is a pure qualitative architecture. According to this, when

a species feeds on multiple prey, none of them dominates it. However, if one prey disproportionately contributes to the predator's energy intake, its extinction would impact the predator, no matter how many other prey species remain. Once the main prey goes extinct, the energy provided by the remaining prey may not be sufficient to sustain the predator. This is what might have occurred to the harp seal, which underwent local extinction through mass migration.

Two seabird species predicted to extinction by the dominator tree were not observed suffering from capelin collapse. This contradiction can reasonably be rooted in the construction of the Barents Sea food web. Probably, information about their diet was only partially complete, and this might have positioned them in the food web with less connection than they really have.

Overall, the comparison between prediction and observation is not completely satisfactory. Validating the dominator tree requires more evidences of secondary extinctions to be compared with model predictions, but this is not easy to do. One reason is that only a few cases of secondary extinctions documented in the literature are accompanied by the detailed information required to build up the food web. The other reason is that the real potential of the dominator tree stands in the possibility of forecasting non-trivial secondary extinctions of species that are separated many trophic steps from their dominator in the food web. These cases are hardly available in literature because the causality relation would be blurred by the complexity of the food web: no one would classify these cases as secondary extinctions because to correctly interpret the results one should use methods such as the one explained in this work. It is not by chance, in fact, that all secondary extinctions documented in the literature involve direct predator–prey relationships. The presence of long pathways of indirect interactions, in the absence of a model that highlights such interactions, makes it difficult to perceive that the disappearance of one species is responsible for the extinction of another that is located many trophic steps away from it. Such cases would be reported as unrelated extinction events, rather than be considered as secondary extinctions.

5. CONCLUSIONS

Dominator trees are simple structures that forecast the effects of species removal because they simplify the food webs by pruning away all pathways that are not fundamental for energy distribution. The potential of this model has been tested using a case study focused on the observed consequences of capelin collapse in the Barents Sea ecoregion. Results highlight that although some correspondence between prediction and observation was found, more studies are required to confirm that the dominator tree can be useful for practical applications. Nonetheless, this study has provided interesting insights that can help directing further analysis. First, link quantification in food webs may increase the correspondence between observations and predictions because a species does not feed equally on all its prey items and may rely on one main prey whose disappearance can put its survival at risk

(Allesina *et al.* 2005). Qualitative dominator trees account for the minimum damage that can occur de facto, that is to say a predator with no prey will go extinct. Second, predator switching can be easily included by considering a food web of potential connections (i.e. including all potential prey, and not only the observed ones), and examining these 'potential food webs' for secondary extinctions. Third, the search for cases to be used in this validation process may help to identify situations of secondary extinction previously unrecognized as such: those in which species that have disappeared were not perceived as functionally linked to one another because of their distance in the food web. In this sense, the dominator tree may contribute to highlight fundamental interactions dispersed in the ecosystem's complexity.

The model of dominator tree is not the only approach to robustness. Other methods have been developed that make use of structural properties of food web such as connectedness (Dunne *et al.* 2002), degree distribution (Montoya & Solé 2003) and expansibility (Estrada 2007) to cite some. These approaches shed light on robustness as a whole system property, intended as resilience against species removal due to random extinctions and/or intentional attacks. Besides that, knowing the fragility of real food webs according to these methods has been indicated as a reliable strategy for *a priori* identification of keystone species, those that have large effects on other species (Solé & Montoya 2001).

The main difference between these methods and the dominator tree model resides in the way they make predictions. Dominator tree holds a true anticipatory value, whereas other methods cannot predict consequences of extinctions until a node is removed from the web. The dominator tree, on the contrary, reshapes the web according to dominance relations between the nodes and, in this way, it allows one to see in advance which nodes are likely to cause the greatest impact on the web if removed. Node removal, on the other hand, is necessary when one works with the other methods. The intricacy of the web does not allow us to immediately identify where a species percolates its effects, so that criteria for removing nodes must be selected at the beginning of the study (i.e. removing species from most to least connected ones, Dunne *et al.* (2002) and Allesina & Bodini (2004)). The lack of anticipatory value of the connectance-based methods is made visible in those cases in which removing the most connected nodes does not produce secondary extinctions (Allesina & Bodini 2004). A promising way to integrate the two approaches is offered by the distinction between functional and redundant connections (Allesina *et al.* 2009). The latter would not contribute at all to food-web robustness so that redesigning the structural approaches by considering only functional links would open up new and interesting perspectives to the study of food-web robustness.

As a final remark, we state that the dominator model can be improved in several directions. Besides the inclusion of link quantification, already discussed, another limitation of the model is that it works well when the initial extinction regards one and only one node. When the initial loss is targeted to more than

one node, cascade extinctions cannot be predicted and a generalized dominator model would better account for these situations. This extended version of the dominator tree model is presently under investigation.

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