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Human impacts on minimum subsets of species critical for maintaining ecosystem structure

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Abstract

Humans have indirectly influenced species at lower trophic levels by driving losses of apex consumers. Furthermore, humans have indirectly influenced species at higher trophic levels by driving losses of primary producers. Beyond these broad classes of apex consumers and primary producers, it remains challenging to identify minimum subsets of species that are particularly important for maintaining ecosystem structure and functioning. Here we use a novel method at the intersection of control theory and network theory to identify a minimum set of driver node species upon which ecosystem structure strongly depends. Specifically, humans could unintentionally completely restructure ecosystems (i.e., change species abundances from any initial values to any final values, including zero) by altering the abundances of these few critical driver node species. We then quantify the proportion of these driver nodes that are influenced by humans, top predators, and primary producers in several marine food webs. We find that humans could unintentionally completely restructure marine food webs while only directly influencing less than one in four species. Additionally, humans directly influence: (1) most or all of the species necessary to completely restructure each network, (2) more driver nodes than top predators, and at least as many driver nodes as primary producers, and (3) an increasing proportion of driver nodes over time in the Adriatic Sea. We conclude that humans have potentially huge impacts on marine ecosystems while directly influencing only the relatively small subset of species that are currently fished. It may be possible to reduce unintentional and undesirable cascading human influences by decreasing human impacts on driver node species in these and other food webs.

Zusammenfassung

Der Mensch hat Arten auf unteren trophischen Ebenen indirekt beeinflusst, indem er Verluste bei Spitzenkonsumenten verursachte. Der Mensch hat aber auch Arten auf höheren trophischen Ebenen indirekt beeinflusst, indem er Verluste bei Primärproduzenten bewirkt hat. Jenseits dieser groben Gruppierungen von Spitzenkonsumenten und Primärproduzenten stellt sich die Aufgabe, die kleinsten Untergruppen von Arten zu identifizieren, die besonders wichtig für den Erhalt von Struktur und Funktion von Ökosystemen sind. Hier nutzen wir eine neuartige Methode an der Schnittstelle von Kontrolltheorie und Netzwerktheorie, um eine Minimalgruppe von Steuerknotenarten zu identifizieren, von denen die Ökosystemstruktur besonders stark abhängt. Insbesondere der Mensch könnte unbeabsichtigt Ökosysteme vollständig umgestalten (d.h. die Abundanzen der Arten von beliebigen Ausgangswerten hin zu beliebigen Endwerten, einschließlich null, verändern), indem er die Abundanzen dieser wenigen entscheidenden Steuerknotenarten verändert. Wir bestimmen dann den Anteil dieser Steuerknoten, die in verschiedenen marinen Nahrungsnetzen vom Menschen, von Gipfelräubern oder Primärproduzenten beeinflusst werden. Wir

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finden, dass der Mensch marine Nahrungsnetze unbeabsichtigt vollständig umgestalten könnte, obwohl er direkt nur weniger als jede vierte Art beeinflusst. Darüber hinaus beeinflusst der Mensch (1) die meisten oder alle Arten, die erforderlich sind, um das Netzwerk vollständig umzugestalten, (2) mehr Steuerknoten als die Top-Prädatoren und mindestens so viele Steuerknoten wie die Primärproduzenten, sowie (3) einen im Laufe der letzten 100000 Jahre zunehmenden Anteil von Steuerknoten im Adriatischen Meer. Wir schließen, dass der Mensch potentiell einen gewaltigen Einfluss auf marine Ökosysteme ausübt, während er direkt nur auf die relativ kleine Gruppe von Arten einwirkt, die gegenwärtig befischt werden. Möglicherweise ließen sich die unbeabsichtigten und nicht wünschenswerten kaskadierenden menschlichen Einflüsse reduzieren, indem der menschliche Einfluss auf die Steuerknotenarten in diesen und anderen Nahrungsnetzen reduziert wird.

Keywords: Food web; Marine; Control theory; Network theory; Fishing; Conservation

Introduction

Humans are influencing natural systems on a global scale (Kareiva, Watts, McDonald, & Boucher 2007; Rockström et al. 2009; Vitousek, Mooney, Lubchenco, & Melillo 1997). For example, species are rapidly going extinct (Barnosky et al. 2011), partly due to over-exploitation of apex consumers (Butchart et al. 2010; Estes et al. 2011). Furthermore, human nitrogen fixation results in widespread N deposition and aquatic dead zones (Vitousek, Aber et al. 1997), and anthropogenic CO_2 emissions are on pace to drive global warming 2 °C above pre-industrial levels (Peters et al. 2013). It remains difficult, however, to predict the cascading effects of such global environmental changes on ecosystem structure (Sala et al. 2000) and ecosystem functioning (Worm et al. 2006). Toward this end, recent studies have identified species (or functional response traits) that are most sensitive to such global environmental changes, and species (or functional effect traits) upon which ecosystem structure and functioning most strongly depend (Isbell et al. 2011; Kirwan et al. 2009; Mori, Furukawa, & Sasaki 2013). Here we use a novel method at the intersection of control theory and network theory to identify subsets of species in marine food webs upon which ecosystem structure strongly depends, and then determine how many of these species are directly influenced by humans.

There is considerable evidence that ecosystem structure and functioning can strongly depend on certain broad groups of species, such as apex consumers and primary producers. Numerous experimental and theoretical modeling studies have found that disrupting top–down (or bottom–up) control of ecosystems can have strong cascading effects to species at lower (or higher) trophic levels (Estes et al. 2011; Gruner et al. 2008; Hillebrand et al. 2007). For example, removing apex consumers can shift communities to an alternative stable state of low biodiversity (Schmitz 2004). Additionally, decreasing the number of plant species can decrease the abundance and diversity of herbivores and carnivores (Scherber et al. 2010). In addition to determining the sensitivity of various ecosystems to disruption of top–down or bottom–up control (Estes et al. 2011; Gruner et al. 2008; Hillebrand et al. 2007), it may also be useful to identify a particular subset of apex consumers, primary producers, or other species upon which ecosystem structure and functioning most strongly depend. For example, the extent to which human influences on apex consumers will cascade to lower trophic levels can depend on the degree distribution of trophic interactions in the food web (Liu, Slotine, & Barabasi 2011). Control theory and network theory can help identify subsets of species that are critical for maintaining ecosystem structure. Counter-intuitively, these do not tend to be the most highly connected species (Liu et al. 2011).

Consider the following linear dynamics of a controlled network (Liu et al. 2011):

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t), \quad (1)$$

where the vector $\mathbf{x}(t)$ describes the state of a system of S nodes at time t. The matrix $\mathbf{A}$, which is $S \times S$, includes elements a_{ij} that indicate the link weight between nodes i and j. The input matrix $\mathbf{B}$, which is $S \times M$, identifies the nodes controlled by the controller. The system is controlled using the time-dependent input vector $\mathbf{u}(t)$, which consists of M unique input signals, and which is imposed by the controller.

Specifically, here we consider humans as an external controller of marine food webs. Let $x_i(t)$ be the biomass of species i at time t, and a_{ij} be the interspecific interaction coefficient describing the net effect of species j on species i, relative to the net effect of species i on itself, as defined by the sensitivity of species i's population growth rate to a change in species j's population density. Let the matrix $\mathbf{B}$ indicate which species humans directly influence and the vector $\mathbf{u}(t)$ indicate the time-dependent direct influences of humans on other species.

The system in Eq. (1) is fully controllable if each node can be individually controlled (Liu et al. 2011). Control, in this case, is defined as the ability to take a system from any initial state to any final state in the state space (including boundaries where one or more species are extinct). For example, humans could fully control food webs by controlling the abundances of all species. It is, however, rarely possible or useful to control all nodes individually. Thus, part of control theory involves identifying a minimum set of driver nodes that could be used to guide the system from some initial state to some other final state (Liu et al. 2011). Although it is unlikely that humans could strategically use driver node species to fully control marine food webs in practice