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Extinction and invasion do not add up in noisy dynamic ecological networks

Yangchen Lin*, William J. Sutherland

Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom

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Abstract

Species extinction and invasion concurrently affect the composition and properties of ecological communities, yet their effects have largely been studied separately, and with more focus on species and ecological functional groups than the whole-community level. We adopted a dynamic ecological network approach to compare the effects of simultaneous single-species primary extinction and invasion on a set of ecosystem metrics to the effects of extinction and invasion in isolation. We also investigated the relationship between the impact and reversibility of extinction or invasion through reintroduction or eradication, respectively. We used Monte Carlo simulations of bioenergetic ecological network models that combined trophic and mutualistic interactions, contained either prey-dependent or ratio-dependent trophic functional responses, and incorporated either white or pink environmental stochasticity. As the separate extinction or invasion impact increased, the simultaneous extinction–invasion impact increased but was decreasingly additive of the two separate impacts, across all ecosystem metrics. Greater extinction or invasion impact was associated with lower reversibility for most model types and ecosystem metrics. There were also systematic differences between models with prey- and ratio-dependent functional responses. These results highlight the importance of considering the combined effects of extinction and invasion in ecological studies, management and restoration.

Zusammenfassung

Extinktion und Invasion von Arten beeinflussen die Zusammensetzung und die Eigenschaften von ökologischen Gemeinschaften, aber ihre Effekte sind meist getrennt untersucht worden, und eher mit einer Fokussierung auf Arten oder funktionelle Gruppen denn auf die Ebene der Gesamtgemeinschaft. Wir untersuchten dynamische ökologische Netzwerke, um die Effekte von gleichzeitigen Ein-Arten-Aussterbe- und Einwanderungsereignissen auf eine Reihe von Ökosystem-Parameter mit den isolierten Effekten von Extinktion und Invasion zu vergleichen. Wir untersuchten auch die Beziehung zwischen Auswirkung und der Reversibilität eines Aussterbe- oder Einwanderungsereignisses durch Wiedereinführung bzw. Ausmerzung. Wir benutzten Monte-Carlo-Simulationen von bioenergetischen ökologischen Netzwerkmodellen, die trophische und mutualistische Interaktionen verbanden, entweder Beute-abhängige oder Verhältnis-abhängige tophische funktionelle Reaktionen enthielten, und

*Corresponding author. Tel.: +44 1223 769018; fax: +44 1223 336676.
E-mail addresses: linyangchen@gmail.com, y.lin@zoo.cam.ac.uk (Y. Lin).

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entweder weißes oder rosa Umweltrauschen einbezogen. Wenn der isolierte Extinktions- bzw. Invasionseffekt zunahm, nahm auch der simultane Extinktion/Invasionseffekt zu, dessen Additivität aus den beiden Einzeleffekten aber abnahm. Dies galt für alle Ökosystem-Parameter. Bei den meisten Modellen und Ökosystem-Parametern waren größere Effekte von Aussterben und Einwanderung mit geringerer Reversibilität verbunden. Es gab auch systematische Unterschiede zwischen Modellen mit Beute- und Verhältnis-abhängigen funktionellen Reaktionen. Diese Ergebnisse unterstreichen, dass es wichtig ist, die kombinierten Effekte von Extinktion und Invasion bei ökologischen Untersuchungen, Management und Renaturierung zu berücksichtigen.
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Keywords: Bioenergetic model; Community dynamics; Ecological network; Environmental stochasticity; Extinction; Food web; Invasion; Noise; Restoration

Introduction

Biodiversity loss is causing changes in ecosystem structure and functioning on a global scale (Hooper et al. 2012), while biotic invasion has been listed as one of the most important global change drivers that influence biotic interactions (Tylianakis, Didham, Bascompte, & Wardle 2008). There has been extensive research on the impacts of extinction and invasion on communities, with the ecological network approach being increasingly used for understanding and predicting impacts on complex ecosystems (Brose 2010).

Numerous studies have dealt with various aspects of food web structure and dynamics as causes (Sahasrabudhe & Motter 2011; Stouffer & Bascompte 2011; Schneider, Scheu, & Brose 2012; Säterberg, Sellman, & Ebenman 2013) and consequences (Berlow et al. 2009; Riede et al. 2011) of primary and secondary extinctions at different trophic levels. Because whole-network time-series data are scarce, most such studies are theoretical, although the models are usually constructed and parameterized using empirical network topologies and community dynamics. Nevertheless, they provide community- and ecosystem-level insights that are impractical to obtain empirically. Such studies, however, are restricted to trophic interactions. Some recent studies have used empirical data to investigate the consequences of extinction on networks of non-trophic interactions either including (Pocock, Evans, & Memmott 2012) or excluding (Valiente-Banuet & Verdú 2013) trophic interactions, but these studies do not incorporate community dynamics.

The effects of invasive species on ecological networks also constitute an area of increasing research. Empirical studies have progressed from early descriptive studies (e.g. Woodward & Hildrew 2001) to recent analyses of long-term data combined with dynamical simulations (e.g. Layer et al. 2011). Recent theoretical modeling studies have identified predictors of invasion success (Romanuk et al. 2009; Galiana, Lurgi, Montoya, & López 2014) and which measures best predict invasion impacts on large food webs (Aufderheide, Rudolf, Gross, & Lafferty 2013). In terms of the effects of invasion on non-trophic networks, most research has been on bipartite mutualistic networks of pollinators and seed dispersers (reviewed in Traveset & Richardson 2006; Memmott 2009; Burkle & Alarcón 2011) and, as with extinction studies, largely restricted to network topology without community dynamics (e.g. Rodriguez-Cabal, Barrios-Garcia, Amico, Aizen, & Sanders 2013; Traveset et al. 2013). A few studies have examined other kinds of mutualistic (e.g. Sugiura 2010) and parasitic networks (e.g. Vacher, Daudin, Piou, & Desprez-Loustau 2010) restricted to particular pairs of taxonomic groups.

Existing network research on the effects of extinction or invasion has one or more of the following limitations: they do not incorporate community dynamics, the models contain only one interaction type, the models are deterministic, or the metrics of perturbation impact pertain to population – rather than community – or ecosystem-level properties. Indeed, responses of ecosystems as a whole to invasions are much less known than responses of populations or communities (Strayer 2012). Furthermore, the vast majority of studies of the impacts of extinction and invasion on ecological networks have so far examined extinction and invasion in isolation from each other, or at invasion as a cause of extinction (Gurevitch & Padilla 2004). There is a lack of studies looking at the combined effects of simultaneous extinction and invasion driven by separate causes (Wardle, Bardgett, Callaway, & van der Putten 2011). The importance of examining both processes concurrently is suggested by Forys and Allen (2002) empirical study of functional group change caused by extinctions and invasions, and Jackson and Sax (2010) who promulgate the notion of 'biodiversity dynamics' in a changing environment as being the shifting balance between species loss and gain. Indeed, non-native species introduced by humans may mitigate the global 'trophic downgrading' of food webs (Estes et al. 2011; Cucherousset, Blanchet, & Olden 2012).

Little is known about the reversibility of extinction and invasion through reintroduction and eradication, although both are increasingly being carried out in restoration ecology; an understanding of reversibility is crucial to restoration (Kardol & Wardle 2010). Lundberg, Ranta, and Kaitala (2000) found in dynamic models of competitive communities that cascading extinctions could sometimes cause community changes that preclude reinvasion, although they did not include trophic and other types of non-trophic interactions and treated reinvasion as a binary rather than continuous variable. The eradication of invasive species can also have

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