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Parasite species richness and its effect on persistence in food webs

C. Finn McQuaid^{*,1}, Nicholas F. Britton

Centre for Mathematical Biology, Department of Mathematical Sciences, University of Bath, Bath, UK

HIGHLIGHTS

- We model an ecosystem with multiple interaction types.
- We compare the effect of parasite species richness on stability.
- Changes in persistence in the system are greater when mutualisms are prevalent.
- Persistence decreases with species richness due to parasite self-limitation.
- The number of parasite species able to exist in the system is unimodal.

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ABSTRACT

Parasitic species are likely to have a significant effect on the stability of ecosystems. However, little is known of the nature of this effect, with debate over whether it is positive or negative. In previous work it was observed that a mixture of interaction types increases the local stability of a network. Following this, we investigate the consequences for species persistence of replacing host species with parasitic species. We consider systems with varying mixtures of mutualistic and antagonistic interactions, showing that the effect of parasitic interactions on a system depends on both the interaction types present and the levels of parasitism considered. Higher levels of mutualism make a system vulnerable to destabilisation on the addition of parasite species. However, for systems with antagonistic interactions, persistence in the system decreases primarily due to the failure of parasite species to persist. This increases with increasing proportions of parasite species, leading to a peak number of parasite species able to persist. Increasing parasite species richness does not have as significant an effect on host species richness as we might expect; although parasites have an important role to play in ecological networks, their effect on persistence is seen primarily through their own self-limitation.

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1. Introduction

Recently, Mougí and Kondoh (2012) demonstrated the surprising effect of considering multiple interaction types, both mutualistic and antagonistic, on the stability of networks of species interactions. It was observed that a mixture of interaction types led to an increase in local stability of a system compared to networks with one interaction type only. Similarly, the presence of parasite species is known to have an important impact on networks of species interactions. In this paper we consider the effect that parasite species richness has on a different metric for stability; species persistence. The importance of interaction type is an area of much interest in the literature, where it is increasingly becoming clear that trophic food webs and networks

with only one interaction type, typical of the majority of previous studies, are unsatisfactory descriptions of species dynamics in an ecosystem (Fontaine et al., 2011; Kéfi et al., 2012). Real ecological networks are composed of species which interact ecologically and evolutionarily with one another in many different forms; as predators, prey, mutualists, competitors, hosts, parasites and so on. Considering one interaction type alone can fundamentally change the network architecture that favours stability (Thébault and Fontaine, 2010), and it is therefore necessary to consider multiple types simultaneously. On the other hand, considering only a bipartite sub-network of a certain class of interaction in isolation, such as a host-parasite or mutualistic system, also fails to capture the realities of species interactions, and enforces a pattern of thinking that may omit vital community dynamics (Olf et al., 2009).

As an example of this, mutualistic interactions between ants and aphids can affect the aphid-parasitoid network, causing a shift from generalist to specialist species (Sanders and van Veen, 2010). Environmental factors may also be important, such as in a host-parasite planktonic system where nutrient enrichment can affect

* Corresponding author. Tel.: +44 1582 763133x2171.

E-mail addresses: finn.mcquaid@rothamsted.ac.uk (C.F. McQuaid), n.f.britton@bath.ac.uk (N.F. Britton).

¹ Present address: Computational and Systems Biology Department, Rothamsted Research, Harpenden, UK.

host dynamics and lead to population cycles, altering probability of parasite persistence (Gerla et al., 2013), and parasites may influence the network structure and stability in turn, as can be observed when a decline in amphibians due to disease alters important ecosystem processes (Whiles et al., 2013). A final example demonstrates the benefits that considering multiple interaction types might offer, where it is suggested that this might allow ecologists to jointly manage pest control and pollination in agroecosystems (Fontaine et al., 2011).

Selakovic et al. (2014) address the importance of parasitic species on interactions throughout an ecosystem, while a good review of the necessity for considering multiple interaction types simultaneously, together with the importance of interaction type and intimacy on network architecture, may be found in Fontaine et al. (2011). Finally, a suggested approach to tackling the inclusion of multiple interaction types may be found in Kéfi et al. (2012).

The inclusion of multiple interaction types when considering ecological networks can have extensive consequences on factors such as the stability and structure of the network, as each interaction type has different effects on these measures (Allesina and Tang, 2012). The addition of parasitic species, without which ecological networks are incomplete, may alter the connectance and nestedness of a system, and therefore have consequences both for its robustness and its stability (Dunne et al., 2013; Freeland and Boulton, 1992; Lafferty et al., 2006). Parasites can regulate host populations, and change many other theoretical properties of food webs that affect our understanding of them (Marcogliese and Cone, 1997). The introduction of parasites to a food web can also drive large changes in network structure (Britton, 2013), as witnessed in the fish species of a subarctic lake (Amundsen et al., 2013). In addition to this, the use of drugs on humans and animals (where coinfection with many parasites is ubiquitous) to eliminate certain parasite species could have an effect on the dynamics of other parasites within these hosts. This is a secondary aspect to drug use that concerns the effects of multiple interaction types, and it has only recently begun to be considered (Knowles et al., 2013).

Efforts have previously been made to include parasitic and other interaction types into the consideration of entire ecological networks, with mixed results. Joppa and Williams (2013) have used a niche model (see Williams and Martinez, 2000) to include both antagonistic and mutualistic interactions in ecological networks, and although their accuracy decreases with network size, empirical properties across networks can often be closely approximated. It has also been suggested that the addition of parasites to food webs could increase their stability (Byers, 2008; Freeland and Boulton, 1992), although this may depend on the life-cycle of the parasite. If the life-cycle is simple, the parasite could be stabilising, while if it is trophically transmitted it could have a destabilising effect (Morand and Gonzalez, 1997). In addition, parasites could make food webs much less “robust”, or resilient to secondary extinctions (Chen et al., 2011; Lafferty and Kuris, 2009). In general, it is known that the addition of parasites increases chain length and alters body-mass ratios, as well as introducing long loops of weak interactions as a result of complex life-cycle dynamics. Energy transfer from prey to predators may be reduced due to parasites, and population levels of common host species may be reduced due to the density dependence of parasites (Lafferty et al., 2008). Although all of the above will have an effect on the stability of a system, how exactly this occurs and the overall net effect is still often regarded as unclear.

Recently, Mougi and Kondoh (2012) addressed a similar problem regarding the mixing of antagonistic and mutualistic interaction types (see also Freeland and Boulton, 1992). They came to the conclusion that a mixture of interaction types increased the stability of a system. Although this conclusion may have been a result of the rescaling of interaction strengths (Suweis et al., 2013), the concept remains interesting. Here we propose a model of a

similar interaction network that includes parasitic interactions, and assess the effect that this has on the stability of the system. Unlike Mougi and Kondoh (2012), we do not investigate the local stability, but focus on the stability measured through the community persistence (see, for example, Brose et al., 2006 and James et al., 2012).

It is likely that linear stability analysis, as used in Mougi and Kondoh (2012), is not applicable to population dynamical equations off food webs, as real-world ecosystems are unlikely to be close to an equilibrium (Drossel and McKane, 2005). However, the community persistence that we consider here ensures that we can compare how many species are able to coexist in a system without being forced to extinction, which is a meaningful and comparable measure (see, for example, James et al., 2012). In addition to this, checking for local stability in the same manner as Mougi and Kondoh (2012) requires defining population growth rates (which can be negative if a species is not basal) such that the system is at equilibrium. In a parasitic system the equivalent term, rate of recovery from infection, can only be positive, artificially limiting the parameter values for which the system can be at equilibrium. A third measure of stability that we do not consider here either is permanence (see Hofbauer and Sigmund, 1989; Jansen, 1987; Law and Blackford, 1992), a measure of the ability of species to increase when rare in a Lotka–Volterra type system, and hence to avoid extinction. Permanence is less limiting than local asymptotic stability, as it allows for systems with chaotic behaviour or limit cycles, similar to real ecosystems, to be classified as stable. However, it does have very stringent requirements for systems to be stable, considering all possible boundary points, which may not be the case in nature for a real “stable” system, and it also allows for very small population densities where in reality extinction might be observed (Law and Blackford, 1992). For further discussions on different types of stability, see Anderson et al. (1992); Chen and Cohen (2001) and Townsend et al. (2010), and for recent remarks on how this may relate to the diversity–stability debate, see Ives and Carpenter (2007) and McCann (2000).

We follow the method of Mougi and Kondoh (2012) in constructing a model with varying proportions of parasitic interactions, and we test this over mutualistic, antagonistic and mixed systems. We predict that the addition of parasites should decrease stability in our systems, as this is akin to the addition of top predators.

In general, we see that, as predicted, the overall levels of persistence in a system decrease across all interaction types with the addition of parasites. However, this does not tell the whole story. We discover that the effects of parasitism on the persistence of host species depends on the interaction types that those species have, and while mutualists decrease in persistence on the addition of parasitic species, systems with mixed or predator-prey-only interactions experience relatively little change. This difference is reduced as the proportion of parasitic species increases. Parasite persistence is likewise affected by the interaction type of the network, with very little change in persistence even at high levels of parasitism in a predator-prey system, although other systems see significant decreases in persistence. This leads to a peak in the number of parasitic species able to persist in our system when the initial network is roughly two thirds parasitic. These patterns are more evident when few mutualist species are present. When the system is composed entirely of mutualistic host species, with very few parasitic species, the results become less predictable and smooth.

2. Methods

Our model is based on that of Mougi and Kondoh (2012). Their model is a Lotka–Volterra system for N species with population

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