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Parasite species richness and its effect on persistence in food webs

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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.

Keywords: stability, interaction type, ecosystem, mutualism

1. Introduction

Recently, Mougi 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 article 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

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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 (Olff 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 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 of 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 densities H_1 up to H_N, and is given by

$$\frac{dH_i}{dt} = H_i\left(r_i - s_i H_i + \sum_{k=1}^{N} a_{ik} H_k\right).$$

The per capita birth rates r_i and density-dependent death rates s_i are chosen from $U(0,1)$, the uniform distribution between 0 and 1. The relationship between H_i and H_k is either mutualistic (with interaction coefficients $a_{ik} > 0$ and $a_{ki} > 0$) or of predator–prey type (with $a_{ik}a_{ki} < 0$); no cannibalistic or competitive interactions (with $a_{ik} < 0$ and $a_{ki} < 0$) are included. In addition, the interactions are structured according

to the cascade model (Cohen et al., 1990), so that there is a random trophic ordering on species, and species are only able to consume those lower in the ordering than themselves. In other words, for $i,k = 1, ..., N$ and $i < k$, species k may consume species i, while species i may never consume species k.

The signs of the interaction coefficients a_{ik} are first chosen to give a specified fraction of mutualistic relationships but otherwise at random, after which the negative interaction coefficients are chosen from $U(-1, 0)$ and the positive ones from $U(0, 1)$. However, the interaction coefficients for each species is inversely proportional to the number of interactions it has with resource species, so a greater number of resources for a species implies that interactions with these will be weaker, i.e.

$$a_{ik} \propto b_{ik} \Big/ \sum_{m \in \text{resource species of } i} b_{im},$$

where b_{ik} is the preference for interaction between species i and k. Finally, not all species interact with one another. Only a certain proportion of the maximum number of potential links are realised, and the remaining interaction coefficients are zero ($a_{ik} = 0$ for species i, k not interacting).

This underlying system contains no (micro)parasites. It is supplemented with P (micro)parasitic species, where each host species H_i may be infected by any of the P parasitic species. Uninfected hosts of species i are denoted by S_i, and hosts of species i infected by parasites of species j by I_{ij}. Coinfections are not considered, so that $H_i = S_i + \sum_{j=1}^{P} I_{ij}$. Parasites may be transmitted both horizontally (with mass-action incidence) and vertically, and infections are taken to be of SIS type, so that the equations become

$$\frac{dH_i}{dt} = H_i \left(r_i - s_i H_i + \sum_{k=1}^{N} a_{ik} H_k \right) - \sum_{j=1}^{P} \gamma_{ij} I_{ij},$$

where

$$\frac{dS_i}{dt} = S_i \left(r_i - s_i H_i + \sum_{k=1}^{N} a_{ik} H_k - \sum_{j=1}^{P} \sum_{l=1}^{N} \beta_j^{il} I_{lj} \right) + \sum_{j=1}^{P} \rho_{ij} I_{ij},$$

$$\frac{dI_{ij}}{dt} = I_{ij} \left(r_i - s_i H_i + \sum_{k=1}^{N} a_{ik} H_k \right) + S_i \sum_{l=1}^{N} \beta_j^{il} I_{lj} - \gamma_{ij} I_{ij} - \rho_{ij} I_{ij}. \tag{1}$$

The per capita birth (r_i) and density-dependent death (s_i) rates depend on the host species i as before, and there is an additional infection-induced mortality rate γ_{ij} of host species i due to parasite species j, as well as recovery rate ρ_{ij}. Infection with parasite species j occurs from hosts of species l to those of species i at rate β_j^{il}. Hosts of species i interact with host species k through coefficient a_{ik}, which may represent an antagonistic or mutualistic interaction as above. Note that both this term and the birth rate imply that vertical transmission of parasites may be possible, as the infected population is increased by both birth and interactions with mutualistic or prey species.

Once again, parameters r_i, s_i, γ_{ij}, ρ_{ij} and β_j^{il} are chosen from $U(0, 1)$ and a_{ik} as previously. Similarly to the restrictions on a_{ik}, infection rates β_j^{il} per host are proportional to the number of host species that a

parasite species infects, which is limited in the same way as the number of links between host species.

Our system initially has $N+P$ species, N hosts and P parasites. We now investigate through simulations how many host and parasite species persist over ecological time. For each specified fraction of mutualistic and parasitic relationships we run 1000 simulations, with parameters chosen at random according to the procedure above and initial conditions for each species chosen from $U(0, 1)$. The proportion each host population that is infected with parasites is chosen from $U(0, 1)$, and the proportion for each parasitic species is chosen using rejection sampling. We run the system for long enough to determine its long-term (asymptotic) behaviour using MATLAB's `ode45` solver, and record the number of host and parasite species that remain above a specified extinction threshold. We refer to this as 'community persistence'.
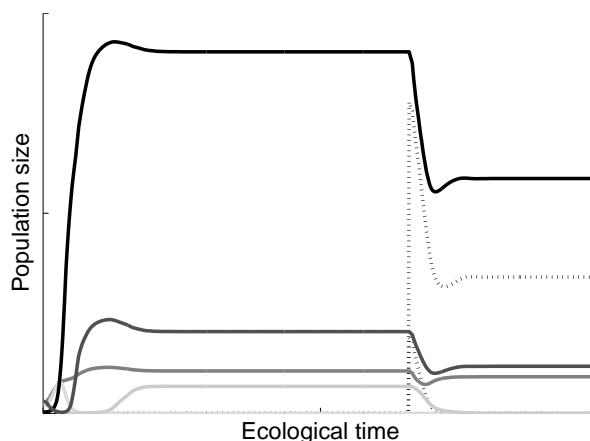
3. Results

Figure 1: Population dynamics of a system with 6 host species before and after the addition of 2 parasitic species. Host species population sizes are represented by solid line of different intensity for each species, while parasite species population sizes are represented by dotted lines. Note that 2 host species are not able to persist in the system at all. Half of host species interactions are mutualistic and half are antagonistic, while 40% of potential connected links are realised and 25% of interactions are parasitic.

In figure 1 we demonstrate the effect that the addition of parasites has on the population dynamics. We note that one host species that was able to persist prior to the addition of parasites is no longer able to persist after their inclusion, hence the level of host persistence in the system decreases. In figures 2 and 3 we investigate this effect over multiple systems for varying proportions of parasitic and mutualistic interactions.

Figure 2 demonstrates the effect that different proportions of parasitic species in systems have on persistence in those systems, differentiating between overall persistence and persistence of host and parasite species separately. In figure 3 we plot the same results as the total number of parasitic and host species that are able to persist for different initial proportions of parasitic interactions. Results for a higher proportion of connected pairs (0.6 compared to 0.4 here) are similar.

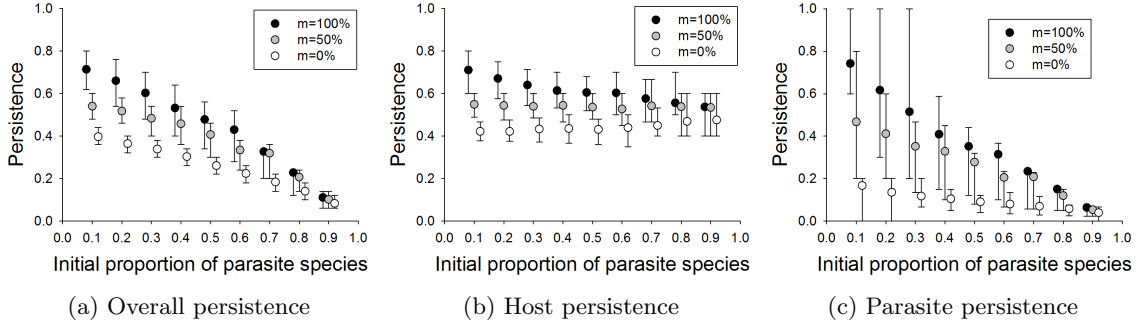(a) Overall persistence   (b) Host persistence   (c) Parasite persistence

Figure 2: Mean community persistence (proportion of species persisting at ecological equilibrium) for ecological networks with different proportions of parasite species, considering the persistence of (2a) the entire ecological network, (2b) host species only and (2c) parasite species only. The percentage of mutualisms in the system increases from 0 to 100% with increased shading intensity as shown in the key. Here we consider for each proportion of parasitic interactions a total of 50 species over 1000 random systems, where bars mark the 25th and 75th percentiles. Parasites target 60% of species, and extinctions are considered to occur if population levels fall below 10^{-4}.

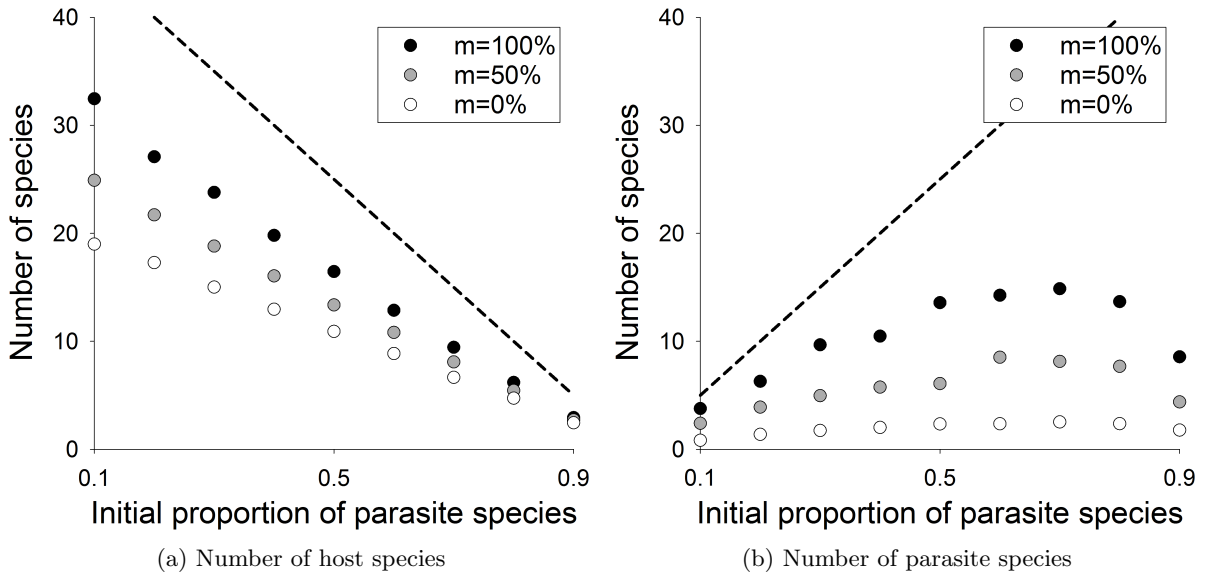(a) Number of host species   (b) Number of parasite species

Figure 3: Average number of (3a) host and (3b) parasitic species persisting for different initial proportions of parasite species in systems with 50 initial species (both host and parasitic). The percentage of mutualisms in the system increases from 0 to 100% with increased shading intensity as shown in the key. In each figure, the dashed line represents the initial number of species (host or parasitic respectively) that began in the system.

Although the overall persistence of the system, as well as the persistence of parasite species, decreases with an increasing proportion of parasitic species, there appears to be very little effect on the persistence of host species in general. We therefore conclude that an increase in proportion of parasites primarily reduces the persistence of parasite species, and that the majority of reduction in persistence of all species in the

network is a consequence of this.

There is, however, still an effect that can be seen on the persistence of host species through the addition of parasite species, which depends on the level of mutualism. When the levels of mutualism are low, then increasing parasite proportion is similar to increasing the number of top predators, and the stability increases very slightly. However, when levels of mutualism in the system are higher, the addition of parasites decreases the persistence of host species. This is similar to the addition of predators to a mutualistic system, which we would expect to reduce persistence as, where there had previously been very little in the way of control in population growth for some species, there could now be a limiting factor due to parasitic-induced mortality (De Castro and Bolker, 2005).

It also appears that systems with higher levels of mutualism have higher levels of persistence, across all levels of parasite species richness, although when host species are mutualistic only, and parasitism is at low levels, then the results become more random and difficult to predict. As the proportion of parasites in the system increases to very high levels, the effect of host species interaction type on host species persistence is reduced, most likely because there are very few host species remaining in the system. This increase in persistence with increasing proportions of mutualisms could be explained by an increase in carrying capacity in the system. As more interactions are mutualistic, host populations may experience higher growth rates, resulting in either increased host population densities or increased parasite densities to balance this. This would mean that parasite species are more likely to have non-negative growth rates, and hence are more likely to persist in the system.

The introduction of additional parasites to a predator-prey network does not come at as large a relative cost in terms of parasite persistence as for a mutualistic or mixed network. In figure 3b, although parasite persistence decreases with proportion of parasites, the actual number of parasites able to persist increases only up to a point. It appears that there is a peak in the proportion of parasites in an initial system which allows for the highest number of parasite species to exist, and the addition of further parasites at a cost to host species richness results in a reduction in parasite species persistence. This suggests that the maximum parasite species richness occurs at around two thirds of the population species richness, after which it is no longer feasible for additional parasite species to invade the system. This peak is more evident the more mutualists there are in a system, while in a predator-prey only system it appears that the number of parasites the system can support is relatively constant.

We note, however, that the unimodal nature of this relationship between parasite species persistence and initial number of parasites could be explained by the substitutive nature of the model with regard to species types, ensuring that the total potential number of individuals that could be infected is decreased. A reduction in the number of host species reduces the carrying capacity of the system, as well as the number of niches available to parasites, while increasing the competition for those niches due to a lack of coinfection. Hence, when the initial proportion of parasitic species is high the initial proportion of host species is low,

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restricting the number of available hosts for infection, and therefore potentially the number of parasitic species able to persist. When the initial proportion of parasitic species is low the number of parasitic species persisting is obviously restricted. This could then result in an intermediate maximum number of parasite species able to persist.

Although the introduction of parasite species simultaneously with the reduction in host species richness may confound the issue, it can be seen in figure 3a that, in general, the replacement of host species with parasites reduces the total number of host species able to persist in an ecosystem, although this is in part caused by the obvious initial decrease in species richness due to replacement with parasitic species. We observe that the slope of the best-fit line for final number of host species *versus* proportion of parasites is always less than the slope for the initial number, implying that the addition of parasitic species has less of an effect for higher proportions of parasitism in the system.

4. Discussion

Addition of parasitic species therefore significantly affects the stability of an ecological network, as expected (Byers, 2008; Dunne et al., 2013; Freeland and Boulton, 1992; Lafferty et al., 2006; Morand and Gonzalez, 1997), and as the addition of mutualistic species does (Mougi and Kondoh, 2012). However, the relationship is not straightforward. The interaction types in the network (mutualistic or antagonistic) alter the proportion of parasites that most favours host species persistence (see also Thébault and Fontaine, 2010). Some studies have investigated persistence for host-parasitoid interactions in small model (Wilson et al., 1996) and real-world (Tuda and Shimada, 2005) systems, as well as the link between a system's stability and parasite species richness (Anderson and Sukhdeo, 2013) and the effects of secondary extinctions (Colwell et al., 2012), but our work provides the first holistic model of the effect of parasites on the stability of an entire ecosystem with many interaction types.

We had anticipated the introduction of parasites to destabilise our model, as parasites may be thought of in some way as top predators. However, although parasites at first glance appear to destabilise the system, as seen in figure 2a, on closer inspection we conclude that this is, in fact, closely linked to a decrease in parasite persistence rather than host species. In addition, the effect of parasites depends on the proportion of mutualisms in the system. A system which is primarily mutualistic will be destabilised by parasites, while one which is primarily antagonistic will, in terms of host species, be relatively unaffected. The addition of parasites also has less of an effect on the relative number of host species when levels of parasitism are already high, and interestingly, we find that there is a unimodal peak in the number of parasites that are able to persist before increasing the proportion of parasites decreases the total number of parasites. The effect of parasitic species on ecological networks, therefore, appears to depend on the nature of the network itself. Unlike the mixing of antagonistic and mutualistic interaction types, there is no one clear effect that the addition of parasites has on the stability of a system. However, this in itself is an interesting and

unexpected observation, and could stimulate future research into why this is the case. The answer to this question could be that we do not see the whole picture in our model. The use of adaptive dynamics to model changing network structures demonstrates that the evolution of the artificial networks we have assumed here changes key network properties such as nestedness over time (McQuaid and Britton, 2013). The interactions assumed between species, a key determinant of their persistence, are not in fact fixed, but are instead a result of dynamic coevolution.

5. Acknowledgements

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