

# On the perils of ignoring evolution in networks

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## On the Perils of Ignoring Evolution in Networks

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Here we reply to the stimulating comments from Sagoff [1] and Rossberg [2] on Segar et al. [3]. Sagoff posits that species assemblages are largely fortuitous and ephemeral, which thwarts opportunities for coevolutionary processes [4]. Given the dynamic nature of ecological communities, have populations from different interacting species had sufficient time in which to generate selective pressure on each other? As Rossberg points out, in long-lasting and highly intimate bipartite networks, “frequent co-occurrence of the two taxa” is required for evolutionary lockstep between **v** (vulnerability) and **f** (foraging) traits. Fitness “seascapes” [2] stem from constant community turnover: but the adaptive troughs and peaks of the shifting seascape can persist and allow reciprocal evolutionary change if allelic turnover is rapid and selection strong enough. How do we specify “frequent co-occurrence”? Since Janzen’s 1985 appraisal of coevolution [4], *Colpoda* protozoans have been through over 53,000 generations: resistance to mosquito predators develops in 50 [5]. We do agree that ecological (non-genetic) fitting is widespread. However, biotic selection within ecological networks does occur, is detectable, and its effects are far from trivial.

## 50 **Empirical support**

Research across a range of systems has demonstrated that microevolutionary change can occur over ecological time scales as populations from different species interact, creating eco-evolutionary feedback loops [6]. In guppies, phenotypic responses to predation intensity, likely with a genetic basis, can occur in a matter of years and the resultant divergence in guppy feeding preferences alters the structure of invertebrate assemblages and local stream food webs [7].

Indeed, the most convincing evidence for the role of evolution in networks is empirical. Loci under selection vary when more than one species is involved: for example, selection for resistance to deer in ivy leaf morning glory, *Ipomoea hederacea*, is stronger when plants are

60 also under attack by insects [8]. The probability and strength of such interactions are in part  
determined by network structure. Ecological context is key, both past and present. Without  
invoking group selection, there is ample evidence that multiple interactants can act in concert  
to produce non-additive selective pressures that influence network structure. For example,  
multiple inter-individual interactions [3] engender diffuse coevolution [9]. It is now widely  
65 accepted that selective pressure originates from multiple sources [10] and that various  
combinations of abiotic and biotic drivers act to shape phenotypic divergence.

It is also apparent that populations from different interacting species do generate selective  
pressure on each other and co-occurrence durations are sufficiently long for evolution to occur.  
This assertion is substantiated by the local adaptations of widespread mutualists (the ‘co-  
70 evolutionary mosaic’) [11]. We do recognize that the persistence of such interactions is likely  
to vary greatly, and accordingly affect the strength of selective pressure. Biotic selection may  
or may not lead to coevolution and subsequent co-speciation, but it can certainly determine key  
parameters such as host use and resistance.

### **Wallace’s line and Darwin’s bridge**

75 Biotic selection can also determine character displacement of phenotypes within interbreeding  
populations and subsequent divergence into non-interbreeding populations (i.e. speciation).  
Such phenotypic divergence can be traced across phylogenies (macroevolution). In other  
words, we must look to Wallace as well as Darwin. Wallace recognised the combined role of  
evolutionary and geological processes in determining the distinct clustering of Earth’s  
80 biodiversity across geographic regions - the regional species pool from which local networks  
are drawn [12]. Descent with modification has shaped the traits through which populations  
interact upon first encounter [2], even if the interacting populations did not evolve together.  
Phylogenetic signal in interactions can therefore determine network structure [2].

We agree with Sagoff [1] that evolutionary processes such as speciation, and spatial ones such  
85 as dispersal, are important co-determinants of the species pool from which networks are  
assembled. Sagoff focuses his critique on microevolution, but the macroevolutionary processes  
determining the generation of species diversity should not be undervalued. As expounded by  
Reznick and Ricklefs [13], Darwin's theory of evolution spans microevolution and  
macroevolution. Individuals within a species can diverge, with some lineages going extinct,  
90 while reproductive barriers build up between others. Biotic interactions are key components of  
the adaptive landscape and speciation process. For example, speciation through ecological  
divergence and evolutionary novelty is common in adaptive radiations. There appears to be  
consensus that speciation is of importance in determining the composition of ecological  
networks. Dispersal is crucial for eco-evolution: it determines population densities and  
95 mediates gene flow, trait mixing and local adaptation. Darwin recognised that dispersal  
contributes as much as the biotic environment in determining species distributions. We  
consider these processes concurrently, hence allowing the data to gauge the role of evolution  
in networks.

### **Invasion and natural laboratories**

100 Sagoff [1] claims that novel and "heirloom" ecosystems do not differ. On the contrary,  
widespread invasions have repeatedly demonstrated that networks can be rendered novel,  
simplified and "rewired" following either the introduction of pre-adapted species with which  
they have not evolved, or human-induced extinction of native species [14,15]. Take invasions  
on islands, for example. Further, human-mediated species invasions have led to the biotic  
105 homogenization of Earth, reducing the potential for demographic or evolutionary rescue.  
Selection for traits that raise the likelihood of successful invasion may take place in the native  
range, so that evolutionary history can be an effective predictor of network persistence.

Evolution can be rapid in trophic interactions and occur more broadly across communities [6] with no requirement for long-term phylogenetic associations.

110 To conclude, Rossberg's [2] formalisations and models provide a welcome path for further insights into our questions. Sagoff [1] seems to impose a stark choice between either a Gleasonian world in which species are independent in traits and distributions, co-occurrences are entirely fortuitous and interactions are of no evolutionary consequence, or a naïve pan-evolutionary world which is entirely structured by simple pairwise coevolutionary processes.

115 Our proposed framework [3] fits neither oversimplified extreme: we seek a richer, more realistic and more fruitful combination of theory and documented network features in order to advance our understanding of how these come to be, are maintained and can be modified. We ignore evolution in ecological networks at our peril.

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