

On the perils of ignoring evolution in networks

by Segar, S.T., Fayle, T.M., Srivastava, D.S., Lewinsohn, T.M., Lewis, O.T., Novotny, V., Kitching, R.L. and Maunsell, S.C.

Copyright, publisher and additional Information: This is the author accepted manuscript. The final published version (version of record) is available online via Elsevier. This version is made available under the [CC-BY-ND-NC licence](#)

Please refer to any applicable terms of use of the publisher

[DOI link to the version of record on the publisher's website](#)



**Harper Adams
University**

On the Perils of Ignoring Evolution in Networks

Simon T. Segar^{1,2,3*}, Tom M. Fayle^{1,2,4}, Diane S. Srivastava⁵, Thomas M. Lewinsohn^{6,7}, Owen T. Lewis⁸, Vojtech Novotny^{1,2}, Roger L. Kitching⁹, Sarah C. Maunsell¹⁰

5 ¹ Biology Centre, Czech Academy of Sciences, Institute of Entomology, Branisovska 1760, 370 05 Ceske Budejovice, Czech Republic,

² University of South Bohemia in Ceske Budejovice, Faculty of Science, Branisovska 1760, 370 05 Ceske Budejovice, Czech Republic,

10 ³ Department of Crop and Environment Sciences, Harper Adams University, Newport, Shropshire, TF10 8NB, UK

⁴ Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia,

⁵ Dept of Zoology & Biodiversity Research Centre, University of British Columbia 6270 University Blvd Vancouver BC Canada V6T 1Z4,

15 ⁶ Depto Biologia Animal, Instituto de Biologia, University of Campinas, Campinas 13083-870, São Paulo, Brazil,

⁷ Wissenschaftskolleg zu Berlin, Berlin 14193, Germany,

⁸ Department of Zoology, South Parks Road, Oxford, OX1 3PS, UK,

20 ⁹ Environmental Futures Research Institute, Griffith University, Brisbane, Queensland 4111, Australia

¹⁰ Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, 02138, USA

Corresponding author: ssegar@harper-adams.ac.uk (Simon T. Segar)

25 Twitter Handle: @simonsegar

Address: Department of Crop and Environment Sciences, Harper Adams University, Newport, Shropshire, TF10 8NB

Telephone: +441952815478

30

35

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.

120

125

130

135 **References**

- 1 Sagoff, M. (2020) Ecological Networks: Response to Segar et al. *Trends Ecol. Evol.* DOI: 10.1016/j.tree.2020.04.008
- 2 Rossberg, A.G. (2020) What Are the Fundamental Questions Regarding Evolution in Ecological Networks? *Trends Ecol. Evol.* DOI: 10.1016/j.tree.2020.06.004
- 140 3 Segar, S.T. *et al.* (2020) The Role of Evolution in Shaping Ecological Networks. *Trends Ecol. Evol.* 35, 454–466
- 4 Janzen, D.H. (1985) On Ecological Fitting. *Oikos* 45, 308–310
- 5 terHorst, C.P. *et al.* (2010) Evolution of prey in ecological time reduces the effect size of predators in experimental microcosms. *Ecology* 91, 629–636
- 145 6 Koch, H. *et al.* (2014) Why rapid, adaptive evolution matters for community dynamics. *Front. Ecol. Evol.* 2,
- 7 Bassar, R.D. *et al.* (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proc. Natl. Acad. Sci. USA* 107, 3616–3621
- 8 Stinchcombe, J.R. and Rausher, M.D. (2001) Diffuse Selection on Resistance to Deer Herbivory in the Ivyleaf Morning Glory, *Ipomoea hederacea*. *Am. Nat.* 158, 376–388
- 150 9 Janzen, D.H. (1980) When is it coevolution? *Evolution* 34, 611–612
- 10 Palacio, F.X. *et al.* (2020) Selection on fruit traits is mediated by the interplay between frugivorous birds, fruit flies, parasitoid wasps and seed-dispersing ants. *J. Evol. Biol.* 33, 874–886
- 155 11 Anderson, B. and Johnson, S.D. (2007) The geographical mosaic of coevolution in a plant-pollinator mutualism: coevolution between mutualists. *Evolution* 62, 220–225
- 12 Wallace, A. (1876) *The Geographical Distribution of Animals, 1876.* Hafner, New York
- 13 Reznick, D.N. and Ricklefs, R.E. (2009) Darwin’s bridge between microevolution and macroevolution. *Nature* 457, 837–842
- 160 14 Mathiasson, M.E. and Rehan, S.M. (2020) Wild bee declines linked to plant-pollinator network changes and plant species introductions. *Insect Cons. Div.* In Press,
- 15 Simberloff, D. (2005) Non-native Species DO Threaten the Natural Environment! *J. Agr. Environ. Ethic.* 18, 595–607