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REVIEWS

foraging traits f_0 [4,13], dietary diversity [3,4], and predator–prey mass ratios [15]. One should therefore ask: does this mean that consumer behaviour and body plans are fundamentally determined at the ecosystem level?

Acknowledgments

This work was supported by the Natural Environment Research Council (NE/T003510/1).

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https://doi.org/10.1016/j.tree.2020.06.004

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Letter

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 vulnerability (v) and foraging (f) 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 (nongenetic) fitting is widespread. However, biotic selection within ecological networks does occur, is detectable, and its effects are far from trivial.

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 ecoevolutionary 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 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 nonadditive selective pressures that influence network structure. For example, multiple interindividual interactions [3] engender diffuse coevolution [9]. It is now widely 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 'coevolutionary mosaic') [11]. We do recognise 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 cospeciation, but it can certainly determine key parameters such as host use and resistance.

Wallace's Line and Darwin's Bridge

Biotic selection can also determine character displacement of phenotypes within interbreeding populations and subsequent divergence into noninterbreeding 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 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 as dispersal, are important codeterminants 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, 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 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

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 preadapted 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 homogenisation of the 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.

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. Our proposed framework [3] fits neither over-simplified 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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https://doi.org/10.1016/j.tree.2020.07.016

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