Misconceptions on the application of biological market theory to the mycorrhizal symbiosis

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Letter to Editor

The symbiosis between plants and arbuscular mycorrhizal fungi has been described as a biological market based on evidence that plants supply more carbohydrates to fungal partners that provide more soil nutrients, and vice versa[1–4]. Walder & Van der Heijden's (WH) recent paper challenges this view[5]. However, WH's challenge is based upon misunderstandings of biological market theory, and evolutionary theory more generally.

First, WH's claim that biological market theory requires (or assumes) tightly-coupled direct resource exchange is incorrect. All that is required is that individuals have a preference *on average* for interacting with more beneficial partners[6–9]. Biological market theory makes no claim on understanding (proximate) mechanisms of transfer processes. This is not its aim. Instead, biological market theory addresses ultimate questions such as why partnerships remain stable over evolutionary time, even in the presence of less beneficial partners. Its usefulness lies in predicting how these exchanges will be affected by context, such as varying environmental conditions[7,8,10–12].

Second, WH suggest that the "most prominent fact" challenging a market-based view of the mutualism is the occurrence of antagonistic or parasitic interactions. However, this claim reveals a key misunderstanding of biological market theory, and mutualism evolution in general. The persistence of some parasitism is actually *expected* under biological market theory, which predicts neither complete disappearance of cheating nor perfect partner choice[8,9,13,14]. In line with this prediction, we observe that parasitic interactions remain a small, but observable, proportion of global mycorrhizal interactions[15].

Third, the authors claim that plant-derived carbon is available to fungal symbionts as a "public good" (*i.e.* individuals cannot be effectively excluded from its use). Both theory and physiology argue against this scenario. Theory unambiguously predicts that symbiotic persistence is facilitated by the evolution of adaptations to exclude less beneficial partners, such that free access to resources is restricted[16–18]. This is backed by physiological evidence of (1) localized carbon delivery to the fungus, namely the evolution of intracellular structures (*e.g.* arbuscules and coils) that facilitate the directed transfer of nutrients, and (2) knockdown and gene-silencing studies suggesting cell-specific nutrient supply determines arbuscule longevity ([19] for review).

Fourth, WH claim that the lack of specificity in the mycorrhizal symbiosis is evidence against the existence of partner choice. This claim is based on a misunderstanding of the existing theory, which predicts the opposite. Biological market theory predicts that low specificity, with a higher number of potential partners, facilitates the evolution of stable trading[6,7,20]. As a host you can gain more when you have the potential to interact with multiple fungal strains, in contrast to being 'locked-in' to one partner[7,20]. This is especially true in variable environmental conditions[10,11].

Fifth, the authors argue that in complex networks (*i.e.* multiple plants and multiple fungi), partner choice may be "difficult and less effective". This claim is likewise based on a misunderstanding of existing theory, which makes the opposite prediction[7]. The authors also argue that "spatial separation may serve as a critical precondition" for discrimination[5]. However, there are mixed findings on the importance of spatial structure, both experimentally[1,2,21] and theoretically[8,21,22], but the variation we find in the precision of partner choice among species[22] and under different conditions[4,24] is actually expected, and again consistent with theory[9] .

Sixth, WH suggest it is a problem that partner identity, environmental conditions, and available external resources all vary in ways that could affect trading choices. But this is not a problem - this is how markets work, both in theory and in practice[6–8,10,11,24]. In contrast to what the authors claim, variable rewards and changing partner preferences are the defining feature of biological markets[6,7,19].

The goal of biological market theory is not to draw analogies to human markets. Rather, biological market theory is a tool to analyse exchange patterns. When applied correctly, it allows scientists to make testable predictions about resource exchange patterns, and how these vary across species and environment[10,12,20,25]. In the past, mycorrhizal researchers could only vaguely refer to "context-dependency" to explain the variability in their results. Biological market theory now allows us to dissect this variability and generate specific and precise predictions for plant-mycorrhizal outcomes[7,8,11,12,20].

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