25th International Congress on Modelling and Simulation, Darwin, NT, Australia, 9 to 14 July 2023
mssanz.org.au/modsim2023

A growth feedback model with limiting resources gives rise to behaviours of mutualism, parasitism, and competition between a plant and a mycorrhizal fungus

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Abstract: Biological mutualism can be defined as a situation where the fitness of two interacting species is increased by the interaction between them (+/+). There is no generally accepted conceptual model of the evolution of mutualisms, or of what mechanisms are necessary for mutualism stability. Plants and soil symbionts, such as mycorrhizal fungi, provide a good system to study the evolution of mutualisms due to examples of mutualism stability and breakdown.

We developed a new model of an individual plant growing in interaction with an individual fungus. The plant and fungus interact and grow over ten time-steps. In each time-step both organisms gather both carbon (C) and phosphorus (P), with the amount of each determined by each organism's size and nutrient uptake efficiency. The organisms then give a proportion of their 'specialised' resource to the other and grow by an amount proportional to whichever resource is most limiting (Liebig's law of the minimum). The nutrient uptake efficiencies of the organisms' 'specialised' resource, C in plants and P in fungi, were set at 100%. The nutrient uptake efficiency of the organisms' 'non-specialised' resource was set between 0 and 100%. These dynamics are described mathematically in equation 1.

$$X_{n+1} = X_n + \min \begin{Bmatrix} \alpha X_n + \epsilon Y_n, \\ X_n(1-\gamma) \end{Bmatrix}$$

$$Y_{n+1} = Y_n + \min \begin{Bmatrix} Y_n(1-\epsilon), \\ \beta Y_n + \gamma X_n \end{Bmatrix} \qquad (1)$$

X plant size	γ plant C share proportion
Y fungi size	ϵ fungi P share proportion
α plant P uptake efficiency	n time step
β fungi C uptake efficiency	

A hill-climb and individual-based evolutionary algorithm were then used to simulate the evolution of sharing strategies between the plant and fungus, with our coupled individual growth model used to determine fitness at each generation. Resource sharing was allowed to be positive or negative and nutrient uptake efficiencies were fixed at various values while evolution was simulated.

We found that with evolution the two species can move from a competitive (-/- fitness interaction) or parasitic (-/+ fitness interaction) relationship into a stable mutualistic (+/+) relationship. We also saw examples of relationships starting as parasitic and moving into a stable competitive relationship and vice versa. When nutrient uptake efficiencies for each organism's 'non-specialised' resource were low, the sharing strategy to produce maximum growth was similar for each organism. However, as the nutrient uptake efficiencies increased in one or both organisms, the sharing strategies for maximum growth became less similar.

Unlike other approaches, our growth model gives rise to competition, parasitism, and mutualism without explicitly coding for these interactions. The assumption of Liebig's law of the minimum together with resource sharing and coupled fitness feedback, can produce stable mutualism. These elements have been largely lacking from previous models, possibly because they are difficult to handle analytically. Our model may be a more suitable base for models of mutualism incorporating behaviours like partner choice than other models that use population level approaches that try to force expected behaviour and outcomes.

Keywords: *Mutualism, modelling evolution, fitness feedback, parasitism, plant-fungus interactions*