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Widespread fitness alignment in the legume–rhizobium symbiosis

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Summary

- Although 'cheaters' potentially destabilize the legume–rhizobium mutualism, we lack a comprehensive review of host–symbiont fitness correlations.
- Studies measuring rhizobium relative or absolute fitness and host benefit are surveyed. Mutant studies are tallied for evidence of pleiotropy; studies of natural strains are analyzed with meta-analysis.
- Of 80 rhizobium mutations, 19 decrease both partners' fitness, four increase both, two increase host fitness but decrease symbiont fitness and none increase symbiont fitness at the host's expense. The pooled correlation between rhizobium nodulation competitiveness and plant aboveground biomass is 0.65 across five experiments that compete natural strains against a reference, whereas, across 14 experiments that compete rhizobia against soil populations or each other, the pooled correlation is 0.24. Pooled correlations between aboveground biomass and nodule number and nodule biomass are 0.76 and 0.83.
- Positive correlations between legume and rhizobium fitness imply that most ineffective rhizobia are 'defective' rather than 'defectors'; this extends to natural variants, with only one significant fitness conflict. Most studies involve non-coevolved associations, indicating that fitness alignment is the default state. Rhizobium mutations that increase both host and symbiont fitness suggest that some plants maladaptively restrict symbiosis with novel strains.

Introduction

Mutualisms are fundamental to ecology and agriculture, with symbiotically fixed nitrogen from the legume–rhizobium interaction providing one-third of the protein in the global human diet (Graham & Vance, 2003) and insect pollination required for three-quarters of crops (Potts *et al.*, 2010). Global change threatens many of these fundamental services through habitat loss, the introduction of novel species and the alteration of the abiotic environments in which species interact, yet we are only beginning to understand the evolutionary forces that shape mutualisms and govern their ability to respond to a changing world (Kiers *et al.*, 2010). The interaction between legumes, species in the family Fabaceae, and the polyphyletic group 'rhizobia', which includes members of alpha-proteobacteria and beta-proteobacteria (Velázquez *et al.*, 2010), is a model system for understanding the ecological and evolutionary basis of mutualism (De Mita *et al.*, 2007; Heath, 2008; Kiers & Denison, 2008). Multiple species' genomes of both the legume host and the bacterial symbiont have been or are in the process of being fully sequenced (Mavingui *et al.*, 2002; Young *et al.*, 2006; Amadou *et al.*, 2008; Sato *et al.*, 2008; Schmutz *et al.*, 2010; Branca *et al.*, 2011; Young *et al.*, 2011) and there are many genetic tools to dissect the molecular basis of symbiosis in these organisms (Ané *et al.*, 2008; Young & Udvardi, 2009; Friesen & von Wettberg, 2010).

The ecological definition of mutualism requires that increasing the population size of one partner causes an increase in its partner's population size, whereas the individual-level definition requires that interaction with a mutualist partner increases the focal individual's relative fitness (Boucher *et al.*, 1982). The legume-rhizobium interaction shows evidence of both rhizobium inoculation consistently having a beneficial effect on legume growth (Kaschuk *et al.*, 2010) and the growth of a compatible host increasing the relative abundance of rhizobia in the soil (Kuykendall, 1989). However, within an interaction that is mutualistic overall, it is possible for antagonistic coevolution to occur as partners may experience conflicts of interest. The parameters of the interaction that maximize fitness for the host are not necessarily those that maximize symbiont fitness. For example, one common trait of rhizosphere-inhabiting microorganisms is the ability to synthesize the plant hormone auxin (Patten & Glick, 1996), which alters the root : shoot ratio and could deviate from the plant's optimal phenotype (Friesen *et al.*, 2011). In the legume-rhizobium interaction, there may be fitness conflict