

Summary

From an evolutionary perspective, cooperation between species, or mutualism, is a puzzle. After all, all else equal, individuals should be selected to gain the benefits from cooperation without paying the cost. This potential for defection and cheating can undermine cooperation and ultimately lead to the breakdown of mutualistic interactions. How has nature solved the problem of cooperation, allowing mutualisms to evolve?

In this thesis, I have used plant-microbe symbioses to help address this question. Most plant species can form a mutualism with soil fungi called arbuscular mycorrhizal fungi (AMF), exchanging carbon for soil nutrients like phosphorus. In the mutualism of plant and rhizobial bacteria, the bacteria fix nitrogen and provide this to the plant. Both of these mutualisms are of crucial evolutionary, ecological and environmental importance. Yet, the evolution, maintenance and dynamics of cooperation in both these systems is not well understood.

In Chapter 1, I set up the general outline of this thesis and discuss several (theoretical) models of mutualism evolution, including biological market models. On a biological market, partners can detect and reward high-quality contributions to the exchange (partner selection or preferential rewarding), counteracting the incentive to defect and stabilising cooperation. This can result in dynamics similar to those on markets in human economies.

In Chapter 2, I explore if biological market theory can also be applied to microbial mutualism. I conclude that biological markets could also exist in microbial interactions, evaluate potential strategies actors on these 'microbial markets' can employ and argue that biological markets can be a useful model that should be applied in the study of microbial mutualisms.

I then analyse open questions in one of the best described examples of a microbial market, the plant-AMF mutualism. In Chapter 3, I argue that partner selection or preferential rewarding is a key force stabilising cooperation among fungi and plants. Still, many questions remain regarding the strength, effectiveness, evolutionary history and context-dependence of plant preferences for more cooperative AMF remain.

In Chapter 4, I attempt to address one of these and study the effect of variation in atmospheric CO₂-concentrations on the abundance of two AMF species that vary in their quality as partners to the host plant. While I did not directly measure nutrient flows, I find fungal abundance patterns that are consistent with an effect of CO₂-concentration on plant preferences, as expected in biological market theory. I also find indications that this may affect the success of more beneficial AMF over multiple generations, potentially affecting the level of cooperation in a mycorrhizal population.

I then explore a potential limit to biological market models. In Chapter 5, I find priority effects exist among AMF colonising plant roots. This means that the first AMF to arrive can outperform a later arriving, and otherwise competitively superior, AMF species. Priority effects among AMF potentially have important implications, including effects on the effectiveness of preferential rewarding and of mycorrhizal inocula in agriculture.

In Chapter 6, I create an evolutionary game theory model to understand why some mutualists specialise on providing a single service or resource, while other provide many different ones. I find that strong trade-offs between mutualistic services and high symbiont numbers favour a division of labour among specialised symbionts but potentially undermine cooperation. Partner selection can stabilise cooperation in these cases and thereby affect not only the level but also the nature of symbiont cooperation.

I then take a historical perspective on mutualism evolution. In Chapter 7, I analyse the deep evolution of nodulation in the plant-rhizobial mutualism using modern phylogenetic comparative methods and generating the world's largest database of symbiotic nitrogen-fixing plant species. I find that an ancient (~100 MYA) 'precursor' was crucial in driving nodulation evolution. I show that without this precursor, the origin of which was an extremely rare event, the mutualism could not have evolved and reveal contemporary plant species likely to still retain this precursor.

Lastly, in Chapter 8, I further analyse the 'stable fixers', a special class of nodulating legumes species that I discovered in Chapter 7. I find that hosts are more likely to be stable fixers, where the cooperation with rhizobial bacteria is extraordinarily stable over evolutionary time, if they have high nutrient leaf contents. This suggests that persistence of (resource) mutualisms over millions of years is favoured by high plant nutrient demands, which increase the benefit of engaging in a mutualistic interaction.

In summary, I have contributed to a wide range of open questions in mutualism evolution, from the applicability of an important class of mutualism models to microbes and specifically AMF (Chapters 2 & 3), experimentally disentangling ecological factors that can affect underground mutualism stabilisation (Chapters 4 & 5) to theoretical analysis of the evolution of specialisation and division of labour on mutualistic exchanges (Chapter 6) and elucidating the historical origins, predispositions and persistence of these cooperative interactions (Chapter 7 & 8).