

## A win-win situation: mutualistic relationships

Society is enchanted by cooperation within nature. Romanticised by documentaries like David Attenborough's 'Seven Worlds, One Planet' and explored in heralded works such as 'The Selfish Gene' by Richard Dawkins, this area of study is both fascinating and enigmatic, with many of these relationships yet to be fully understood or even documented. Mutualisms underpin entire ecosystems, as well as humanity's functioning via agriculture, so understanding them is crucial to our, as well as a host of other species', survival of ensuing changes to the planet caused by anthropogenic expansion and climate change.

Before exploring examples of mutualism and the extent to which it is a 'win-win situation', it is first important to define the parameters of mutualistic relationships. Figure 1 illustrates the 'coaction compass', pioneered by Edward Haskell in 1949, two years after his proposition of the 'interaction grid'. Both have come under intense scrutiny, however alternative methods are yet to catch on; variations of these models remain the most favoured method of displaying the myriad of possible interspecific interactions, especially as the coaction compass can quantify the magnitude of the net effect of the interaction<sup>[1]</sup>. However, the coaction compass fails to depict the shift between mutualism and antagonism over evolutionary time<sup>[2]</sup>. Strictly adhering to the grid, mutualism could be defined as any relationship with interspecific

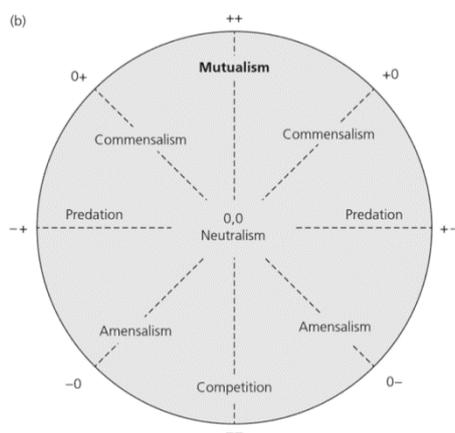


Figure 1- The coaction compass (Haskell, 1949)

interaction with '++' occupation. It is crucial to consider the varying characteristics, however: degrees of dependency (obligate to facultative), specificity (species-specific to generalised), physical integration (symbiotic or non-symbiotic), shared evolutionary history and the nature of the exchanged benefits. In addition to this, recognising that obligacy and specificity are continua rather than dichotomies for the members of an association needs also to be taken into account<sup>[3]</sup>. Put simply, each mutualistic relationship varies in a plethora of ways, and its nature may be different for each organism involved.

Historically, the principle of the 'balance of nature' has always been assumed, but seldom studied in great detail. Herodotus, the 'father of history', recorded the mutualistic relationship between plovers and crocodiles, and later philosophers such as Aristotle drew moral lessons from these 'friendships'. In the West, this theological and perhaps idealistic view of mutualism persisted until the Industrial Revolution, seemingly perfectly aligning as evidence for Divine Providence<sup>[2]</sup>. Laying the foundations of modern conceptions of mutualistic interactions, it was Darwin who discussed the evolutionary mutualism between plants and flowers, chiefly because it appeared to challenge the very theory that he is most famous for: natural selection<sup>[4]</sup>. This apparent disunion between the theory of natural selection and mutualism is pervasive in research in this field of study. Evolutionary theory predicts so-called 'cheaters' in a mutualistic relationship, as it would optimise their own fitness and hence the likelihood of their survival, consequently asserting that mutualisms should not persist if this cheating is uninhibited. This could be explained by discrimination mechanisms that favour a partner who is of higher quality (maximises the returned benefits) over cheaters (minimises the returned benefits)<sup>[5]</sup>. However, this too fails to fully account for the variation within mutualistic relationships. The 'paradox of the market' is as follows: if the choice of partner is effective then the frequency of co-operative partners will increase. This leads to

lower benefits from choice, thus leading to selection against it as the partner choice is a cost rather than a benefit, which as a result allows ‘cheaters’ to encroach again<sup>[6]</sup>. There are a number of ways in which this contradiction is managed within partnerships; I shall focus upon sanctions, negotiations and screening.

The interaction between leguminous plants and rhizobial bacteria involving nitrogen fixing is incredibly well understood at its molecular and physiological level, however the persistence of ineffective strains, indicative of potential cheating, is far more elusive. Rhizobia, a diazotrophic bacteria, possesses the ability unique to prokaryotes to fix atmospheric nitrogen, a limiting factor for its eukaryotic host<sup>[7]</sup>. In return for this fixed nitrogen, the leguminous plant provides nutrients and energy to the rhizobia. This ancient mutualism is theorised to have prevailed due to partner choice via sanctions, in which legume plants can withhold nutrients to the nodules where rhizobia reside, if the bacteria is not fixing enough nitrogen for the partnership to be mutually beneficial. Models for this have concluded that more rigorous sanctions are favoured when a greater abundance of resources are regained as a result of sanctioning, there is a greater variance in the rate of fixation, and that there is a higher mean rate of fixation amongst rhizobial bacteria prior to sanctions being imposed<sup>[8]</sup>. This appears to corroborate the theory that sanctions may favour co-operative behaviour, however, by treating leguminous plants and rhizobia separately, the model lacks explanation for the patterns of variation in fitness arising from sanctions between the plants and bacteria<sup>[6]</sup>.

Johnstone and Bshary explored the persistence of mutualistic relationships, despite the opportunities for cheating, through a model that considers the relative abundance of the cheaters and their ‘victims’, which consequently leads to differences in the time taken for individuals of either type to find a new relationship<sup>[9]</sup>. In the case of cleaner fish removing ectoparasites from larger fish, they found that a low abundance of cleaner fish, the ‘cheater’, led to higher levels of exploitation (eating healthy tissue alongside the parasites), however when larger fish are rare, little to no exploitation occurs. This supports the biological market hypothesis; in the latter case, the cleaner fish encounter a high opportunity cost of causing a larger fish to leave through exploitation as it will take a long time to find a partner due to their rarity<sup>[9]</sup>. Whereas, in the former case, the larger fish are the ones that must endure the high opportunity cost due to the relatively low abundance of cleaner fish. Colloquially, whether it is a ‘buyer’s or seller’s market’ determines the levels of exploitation. It also raises the question of whether the mutualism can be determined a ‘win-win’, as it is difficult to determine a threshold of relative exploitation that when exceeded, the relationship is no longer mutually beneficial. The ecological dynamics here have not yet been fully explored; however current models support that outcomes of mutualisms depend strongly on these outside options<sup>[6]</sup>.

Not associating with a cheating partner via screening mechanisms is an alternative, in order to ensure a ‘win-win’ relationship from its commencement. Rather like job screening, which helps to distinguish between high and low-quality candidates, organisms evolve to create an environment in which only non-cheaters would survive. Archetti et al.<sup>[10]</sup> used the example of the mutualism between *Euprymna scolopes* (Hawaiian bobtail squid) and *Vibrio fischeri* bacteria. Here the squid provides the bacteria with a habitat and nutrients such as amino acids, and the bacteria provides an illuminating blue glow, protecting it from predators by hiding its silhouette, and potentially its circadian rhythm too<sup>[11]</sup>. The squid’s light organ is colonised, wherein the luciferase enzyme, responsible for the bioluminescence, removes reactive oxygen that is harmful to the bacteria<sup>[10]</sup>; therefore, cheating bacterial strains that

would not produce light do not colonise the squid initially, and the problem of parasitism is solved. Altogether, these three mechanisms and their economic analogies provide satisfying rebuttals to the paradox of the market, and how organisms ensure symbioses are ‘win-wins’. Future research is likely to provide further understanding, especially in conjunction with relevant economic models.

Mutualism is not always a ‘win-win’, even when both organisms receive net benefits. Co-dependency can quickly diverge and become coextinction; a negative interaction for all parties involved. In the event of dependency upon another species (from obligate to facultative), population decrease of one causes a positive feedback loop causing the decrease in population of its mutualistic partner, potentially leading to cascading consequences across many trophic levels<sup>[12]</sup>. When the environment is stable, this detriment occurs less frequently, however due to the fragility of many mutualistic interactions, coupled with climate change, the survival of existing mutualisms is under threat. When threshold levels of environmental degradation are exceeded, mutualist networks may disintegrate<sup>[13]</sup>, and due to the increasing levels of biodiversity loss, coextinction rates may increase. There lacks empirical evidence for coextinction of mutualists, due to most interactions not having been documented, and the small size of many organisms involved. Fossil records show evidence of coextinction, for example the extinction of specialised herbivores was preceded by plant extinctions upon which they relied, most likely due to their homogenous diet<sup>[14]</sup>. However, it is unclear if this was also due to the impact of changing environmental conditions, particularly the fallout of the asteroid impact in the Yucatan Peninsula. Therefore, whilst mutualism coextinctions are theorised to be the most prevalent form of biodiversity loss<sup>[12]</sup>, we cannot yet conclusively state their importance as drivers of extinction. Nonetheless, we can infer that mutualists’ simultaneous decline, due to their reliance upon one another, can be viewed as a disadvantage for both species, especially in times of rapid ecological shifts.

Mutualisms are traditionally grouped into three categories: transportation, protection and nutritional mutualisms<sup>[2]</sup>; I have already discussed protection (bioluminescence) and nutritional (legume-rhizobium), so I shall further explore transportation mutualisms, specifically plant-pollinator interactions. Here, there is an exchange in which pollinators receive food via nectar and plants receive efficient vectoring of sexual reproduction by this action<sup>[15]</sup>. Many of these mutualisms are examples of coevolution of species; Darwin himself predicted the existence of a hawkmoth pollinator with a 30cm-long tongue after examining long nectar spurs of the Madagascan star orchid (*Angraecum sesquipedale*)<sup>[16]</sup>. Darwin was ridiculed for this suggestion, however, four decades after his initial proposition, the *Xanthopan morgani* in Madagascar was discovered, and did indeed possess a proboscis of a rather large magnitude<sup>[17]</sup>. His hypothesis of a ‘race in gaining length’, wherein the moths and orchid simultaneously select for longer tongues and spurs respectively, has received greater criticism; this example of reciprocal selection could potentially be adaptations to entirely unrelated environmental pressures<sup>[16]</sup>. This being said, strong empirical evidence for directional selection towards longer tongues for hawkmoths (in order to access more nectar) and longer spurs (in order to achieve more efficient pollination) has

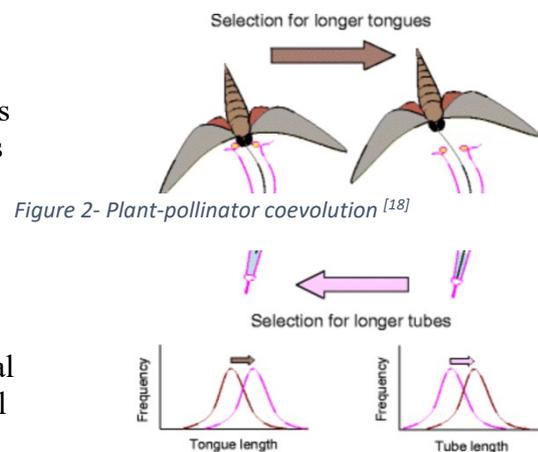


Figure 2- Plant-pollinator coevolution<sup>[18]</sup>

emerged in recent decades, and this ‘escalatory coevolution’ concept (Figure 2) is becoming widely accepted and researched<sup>[18]</sup>. This unique mutualism also demonstrates the array of complementary fields to which the study of mutualism relates.

Researching mutualisms is becoming increasingly critical to conservation efforts to preserve habitats from the ecological shifts brought about by anthropogenic climate change<sup>[19]</sup>. Understanding mutualism response to climactic stress, and how this will reverberate across trophic levels, is important not only to the natural world, but also to humans, as our approximately one-third of our food sources depend upon pollinators<sup>[20]</sup>. Ensuring their survival is therefore imperative to food security. Current research indicates that the greatest challenge for pollinators is diminishing forage<sup>[15]</sup>; climate change imposes selection upon plants and causes a reduction in density. Consequently, the pollinator population cannot achieve positive growth rates<sup>[21]</sup>. This can result in a positive feedback cycle for subsequent generations, especially as climate change is being exacerbated, not reduced. If sufficiently low populations in both mutualists are reached, the mutualism collapses - in obligate mutualisms extinction occurs and in facultative mutualisms, partners often evolve to find different partners<sup>[21]</sup>. Therefore, climate change may result in large-scale destruction of these ‘win-win’ situations and reduce them to no longer being mutualisms. More optimistically, climate change appears to be accelerating the rate of evolution<sup>[22]</sup>, and studying the co-evolution of emerging mutualisms may be an increasingly exciting field of research.

Niamh Toohar

## Bibliography

- [1] R. A. Leary, *Interaction Theory in Forest Ecology and Management*, Springer Netherlands, 1985. Accessed 14/2/21
- [2] J. L. Bronstein, "The study of mutualism," in *Mutualism*, Oxford University Press, pp. 4-17. Accessed 23/2/21
- [3] J. Ollerton, "Biological Barter": patterns of specialization compared across different mutualisms, University of Chicago Press, 2006. Accessed 14/2/21
- [4] D. G. S. M. Massimo Nepi, "Nectar in Plant–Insect Mutualistic Relationships: From Food Reward to Partner Manipulation," *Frontiers in Plant Science*, 2018. Accessed 15/2/21
- [5] J. R. S. Katy D. Heath, "EXPLAINING MUTUALISM VARIATION: A NEW EVOLUTIONARY PARADOX?," *International Journal of Organic Evolution*, vol. 68, no. 2, pp. 309-317, 2013. Accessed 15/2/21
- [6] E. Akcay, "Evolutionary models of mutualism," in *Mutualism*, Oxford University Press, 2015, pp. 57-74. Accessed 16/2/21
- [7] E. F. J. J. P. M. M. L. Teodoro Coba de la Peña, "The Symbiosome: Legume and Rhizobia Co-evolution toward a Nitrogen-Fixing Organelle?," *Frontiers in Plant Science*, 2018. Accessed 16/2/21
- [8] E. T. K. I. P. R. F. D. S. A. West, "Sanctions and mutualism stability: when should less beneficial mutualists be tolerated?," *Journal of Evolutionary Biology*, vol. 15, no. 5, pp. 830-837, 2002. Accessed 18/2/21
- [9] R. B. R. A. Johnstone, "Mutualism, market effects and partner control," *Journal of Evolutionary Biology*, vol. 21, no. 3, pp. 879-888, 2008. Accessed 18/2/21

- [10] F. U. D. F. N. E. P. D. W. Y. Marco Archetti, "Let the Right One In: A Microeconomic Approach to Partner Choice in Mutualisms," *The American Naturalist*, vol. 177, no. 1, pp. 75-85, 177, 2011. Accessed 19/2/21
- [11] C. Arnold, "National Geographic," 25th June 2013. [Online]. Available: <https://blog.nationalgeographic.org/2013/06/25/glowing-bacteria-control-squid-hosts/>. [Accessed 19th February 2021].
- [12] N. C. H. R. K. C. L. P. K. N. S. S. Robert R. Dunn, "The sixth mass coextinction: are most endangered species parasites and mutualists?," *Proceedings of the Royal Society B*, vol. 276, no. 1670, 2009. Accessed 22/2/21
- [13] A. R. I. A. K. E. Toby Kiers, "Global change and mutualisms," in *Mutualism*, Oxford University Press, 2015, pp. 241-263. Accessed 22/2/21
- [14] K. R. J. P. W. Conrad C. Labandeira, "Impact of the terminal Cretaceous event on plant–insect associations," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 99, no. 4, pp. 2061-2066, 2002. Accessed 22/2/21
- [15] G. A. W. Susan W. Nicolson, "Plant–pollinator interactions and threats to pollination: perspectives from the flower to the landscape," *Functional Ecology*, vol. 31, no. 1, pp. 22-25, 2017. Accessed 23/2/21
- [16] B. Anderson, "Coevolution in mutualisms," in *Mutualism*, Oxford University Press, 2015, pp. 107-128. Accessed 23/2/21
- [17] M. McCarthy, "Nature Studies: The Madagascar orchid and the extraordinary moth that goes with it," *The Independent*, 28th April 2014. Accessed 23/2/21
- [18] B. A. Steven D. Johnson, "Coevolution Between Food-Rewarding Flowers and Their Pollinators," *Evolution: Education and Outreach*, vol. 3, pp. 32-39, 2010. Accessed 24/2/21
- [19] M. M. T. H. D. P. C. Rachael Winfree, "Conserving and restoring mutualisms," in *Mutualism*, Oxford University Press, 2015, pp. 268-283. Accessed 24/2/21
- [20] C. L. Landry, "Mighty Mutualisms: The Nature of Plant-pollinator Interactions," *Nature Education Knowledge*, vol. 3, no. 10, p. 37, 2010. Accessed 24/2/21
- [21] N. S. F. K. C. A. N. E. R. R. Tucker Gilman, "Evolution of plant–pollinator mutualisms in response to climate change," *Evolutionary Applications*, vol. 5, no. 1, pp. 2-16, 2012. Accessed 24/2/21
- [22] C. D. Thomas, *Inheritors of the Earth*, Penguin Books, 2018. Accessed 24/2/21