The Abdus Salam
International Centre for Theoretical Physics

2022-23

Workshop on Theoretical Ecology and Global Change

2 - 18 March 2009

Conditional outcomes in mutualistic interactions

HERNANDEZ DE RODRIGUEZ Maria Josefina
*(*BRONSTEIN J.L.)*

*Universidad Central de Venezuela
Instituto de Zoologia Tropical
Facultad de Ciencias, Apartado 47058, 1041-A
Caracas
VENEZUELA*

10 Boecklen, W.J. and Spellenberg, R. (1990) *Oecologia* 85, 92–100
11 Aguilar, J.M. and Boecklen, W.J. (1992) *Oikos* 64, 498–504
12 Fritz, R.S., Nichols-Orians, C.M. and Brunsfeld, S.J. *Oecologia* (in press)
13 Whitham, T.G., Morrow, P.A. and Potts, B.M. *Oecologia* (in press)
14 Whitham, T.G., Morrow, P.A. and Potts, B.M. in *The Ecology and Evolution of Gall-forming Insects* (Baranchikov, Y.N., Price, P.W. and Mattson, W.J., Jr, eds), USDA General Publication, North Central Forest Experiment Station, St Paul, MN, USA (in press)
15 Boecklen, W.J. and Larson, K.C. in *The Ecology and Evolution of Gall-forming Insects* (Baranchikov, Y.N., Price, P.W. and Mattson, W.J., Jr,

eds), USDA General Publication, North Central Forest Experiment Station, St Paul, MN, USA (in press)
16 Floate, K.D. and Whitham, T.G. (1993) *Am. Nat.* 141, 651–662
17 Martinsen, G.D. and Whitham, T.G. *Wilson Bull.* (in press)
18 Hall, R.W. and Townsend, A.M. (1987) *Environ. Ent.* 16, 1042–1044
19 Drake, D.W. (1981) *Aust. J. Bot.* 29, 25–36
20 Coustau, C., Renaud, F., Maillard, C., Pasteur, N. and Delay, B. (1991) *Genet. Res.* 57, 207–212
21 Mason, J.R. (1990) *Wilson Bull.* 102, 160–162
22 Heaney, L.R. and Timm, R.M. (1985) *Biol. J. Linn. Soc.* 25, 301–317

Conditional outcomes in mutualistic interactions

Judith L. Bronstein

Mutualisms are interspecific interactions in which both partners experience a net benefit. Mutualisms are ubiquitous in nature, as well as extremely diverse[1,2]. They range from species-specific, obligate, coevolved associations to looser and more generalized ones, and include relationships both between free-living species (e.g. plants and their pollinators) and species living in close association for their entire lifetimes (e.g. mammals and their gut bacteria). The more intimate mutualisms are often considered separately as 'symbioses', adding to a confusion of terminology that has long plagued the study of beneficial interactions (Box 1). In recent years, however, efforts have been made to identify ecological and evolutionary patterns that cut across diverse forms of mutualism[3–8].

One such generality is that in most mutualistic associations, one partner performs some action (a service) that benefits its associate, and receives some payoff (a reward) for doing so[7]. These rewards are often costly to produce: for example, up to 37% of the photosynthate that the milkweed, *Asclepias syriaca*, assimilates during flowering is used to produce nectar[9]. It can therefore be expected that organisms will minimize these costs by producing as little reward as is necessary to obtain service from their mutualists. Hence, mutualisms are clearly not 'altruistic' (Box 1): they generally last only as long as the benefits of the interaction outweigh its costs to each partner. Most pollinators, for instance, will abandon a plant species once they discover a higher quantity or quality of nectar elsewhere[10].

In the grid of interactions commonly presented in ecology textbooks (Box 2), mutualism is classified simply as a 'plus/plus' interaction. However, when mutualisms are considered from a cost/benefit perspective, it becomes clear that outcomes must in fact be extremely dynamic. If

Interspecific interactions are traditionally displayed in a grid in which each interaction is placed according to its outcome (positive, negative or neutral) for each partner. However, recent field studies consistently find the costs and benefits that determine net effects to vary greatly in both space and time, inevitably causing outcomes within most interactions to vary as well. Interactions show 'conditionality' when costs and benefits, and thus outcomes, are affected in predictable ways by current ecological conditions. The full range of natural outcomes of a given association may reveal far more about its ecological and evolutionary dynamics than does the average outcome at a given place and time.

Judith Bronstein is at the Dept of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.

either the costs or the benefits change in magnitude, then the degree to which an association is mutually beneficial will change as well. Hence, any interaction might be considered to occupy a potentially dynamic position along a continuum of possible outcomes, ranging from beneficial to progressively more antagonistic (Box 2). It is increasingly clear that over evolutionary time, certain interactions have shifted away from antagonism towards commensalism and even mutualism[5]. Researchers are beginning to delineate the genetic and life-history conditions that predispose such evolutionary transitions[11,12]; some of these transitions are being studied with great success in laboratory cultures[13]. Costs and benefits also frequently vary, however, over ecological time and space for a single interaction, leading to what have recently been referred to as conditional outcomes[14,15]. Here, I focus on conditional outcomes of mutualistic interactions, reviewing their origins, patterns of occurrence and evolutionary significance.

Causes of conditional outcomes

The fact that costs and benefits fluctuate does not mean that outcomes of interactions are completely unpredictable for their participants. A number of ecological and life-history factors have been shown partially to determine these outcomes[6,14,16].

Outcomes of a potentially beneficial interaction often depend on the size or age of one of the participants, because either its need for the mutualist's service, or its ability to reward that partner, is stage-dependent. For example, many plants appear to gain protection from herbivory by ants that feed at their extrafloral nectaries (Box 3). However, the magnitude of this benefit is related to plant size, particularly for tree species[17]. Relatively small individuals may produce so little reward that they fail

to attract enough ants to significantly reduce herbivore populations. At the other extreme, larger trees attract many more ants, but they may be unable to patrol the larger surface area thoroughly enough to limit herbivory. To understand the ecology and evolution of interactions, it makes sense to document these relatively poorly known, stage-specific phenomena (or 'distributed outcomes'), rather than to calculate some hypothetical net outcome for the 'average' individual within the population[6].

Outcomes of mutualisms also vary with the abiotic and biotic setting in which the interaction takes place. The ability of mutualists to produce high-quality rewards for their partners may be resource-limited: for example, watering certain plants can increase volumes and sucrose concentrations of floral nectar[18]. The need for the mutualistic service can also vary with resource availability, particularly when the mutualist itself is the provider of some limiting nutrient. For instance, association with mycorrhizal fungi augments certain plants' limited supply of phosphorus, at the cost of a certain amount of photosynthate 'fed' to the mycorrhizae[19]. Plants reduce or even eliminate their mycorrhizal infections when phosphorus is added to the soil[19], suggesting that their costs to host plants exceed their benefits under nutrient-rich conditions. Parallel phenomena are known from other symbiotic mutualisms involving nutrient provision[20].

The local biotic environment, that is, the identity and abundance of other species with which the mutualists interact, also strongly influences outcomes. Costs and benefits of ant–herbivore mutualisms (Box 3) can vary with the species and condition of the herbivores' host plant[14,16,21]. When the service that mutualists provide is protection from predators or parasites, the abundance of those enemies will determine whether protection is needed at all. For example, several groups of fish are well known to 'clean' other fish species by feeding on their ectoparasites[22,23]. However, foraging by cleaners often damages the scales of their hosts, making the net outcome of this interaction antagonistic at times and places where parasite loads are low. In fact, it has been questioned whether this interaction is ever mutualistic[23].

Finally, local abundances of the mutualists themselves can influence the outcome of their interactions. Per-capita benefits often increase as mutualist populations grow but then shift downwards again at large population sizes[3,6,14,24]. In other cases, the cost of rewarding mutualists becomes excessive when they become overabundant. Species inhabited by nutrient-providing unicellular organisms often have mechanisms that limit population growth of these symbionts[25], implying that excessive infections are costly to hosts.

Conditional outcomes in an ant–membracid mutualism

Although the existence of conditionality is generally acknowledged, studies describing the range of outcomes likely to be found in any one interaction are still remarkably few. One exception is the recent work of Cushman and Whitham[15,26] on a conditional mutualism between an ant, *Formica altipetens*, and membracid, *Publilia modesta*, in northern Arizona, USA. Membracids (treehoppers) are homopteran phloem-feeders; the ants protect the aggregated membracids from their natural enemies, while harvesting their energy-rich excretions (Box 3).

Cushman and Whitham[15] first examined whether or not the average benefit of ant protection was consistent from year to year, and whether or not this benefit was independent

Box 2. Forms of interspecific interaction

The usual means to depict forms of interspecific interaction is as a grid, in which each interaction is placed according to its net consequences (positive, negative or neutral) for each partner.
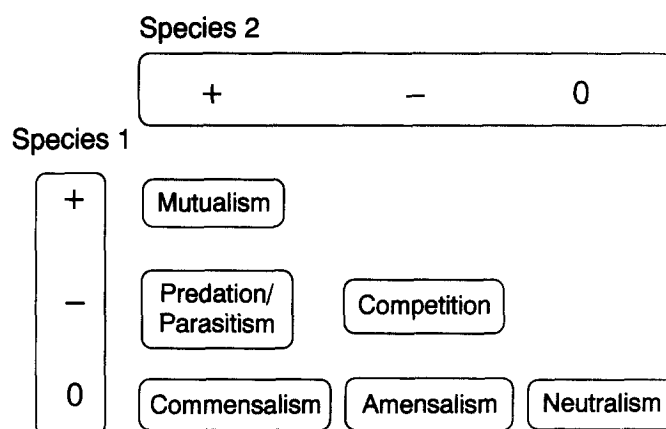
Mutualisms are placed into the (+,+) quadrant. The (+,–) quadrant is occupied by predator/prey, host/parasite, and host/pathogen interactions; these associations, together with competition (–,–) and amensalism (–,0), are often referred to as *antagonisms*[5].

Recently, however, this grid has been heavily criticized for its static, typological presentation of interactions[6,14,37,39]. In reality, interactions occupy different quadrants of the grid at different places or times; they also vary in intensity. It may thus be more accurate to depict interactions as occupying potentially dynamic positions along a continuum of possible outcomes[6,14,16,37]. Here is an example of one of many such continua, ranging from mutually beneficial (at its midpoint) to strongly beneficial for one partner but detrimental for the other (at its endpoints):
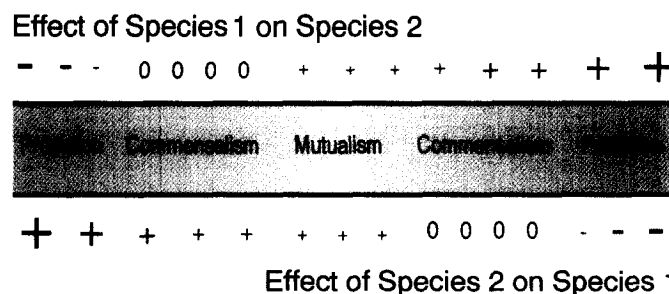
If the outcome of a given interaction is set by the balance of costs and benefits of association for each partner, then the magnitude of those consequences (strong or weak) and even their sign (positive, negative or zero) should shift if the magnitudes of costs and benefits change. As discussed in the text, such shifts along the continuum can occur either at an evolutionary or ecological timescale as well as over space, and may be correlated with a variety of ecological and life-history variables.

Box 3. Ant protection mutualisms

In one common form of mutualism, a food reward is exchanged for protection from one's enemies. Protection in these cases results from aggressive defense of the food, and thus the food producer. Ants are particularly common and effective defenders, a probable consequence of their dietary preferences, aggressive habits, natural abundance and adaptations for rapid recruitment of colony members to rich food resources[5,33]. Most ant protection-mutualisms are facultative and probably only loosely coevolved[15,26,33], although certain more-specific relationships have been well-documented[32,33].

Ants defend both plants and herbivorous insects. Many plants produce nectar from extrafloral nectaries (secretory organs found in a variety of locations away from the flowers). Ants avidly collect extrafloral nectar; some of them effectively patrol the plant, attacking and chasing away other visitors, including certain herbivore species. In some (but by no means all) cases, the resultant decrease in herbivore damage increases plant fitness[33]. Ants also defend a variety of herbivore species. For example, many Homoptera, including aphids, membracids and scale insects, feed on plant phloem and excrete waste fluids ('honeydew') rich in sugars and amino acids. Ants collect this food resource and defend it by attacking the homopterans' predators and parasites. As discussed in the text, the quantity and quality of protection that ants provide change with their mutualists' host plant and aggregation size, as well as with local abundance of their predators.

---

of a membracid's age. Membracid survivorship was compared between host plants (*Helenium hoopseii*, Compositae) naturally infested with ants and hosts from which ants had been excluded. In 1985 and 1987, ant exclusion resulted in a 54–68% decrease in the mean number of membracids per plant. However, no effect of ants was detected in 1986. The difference was not the result of ant abundance, which was fairly constant over time. Rather, a major predator (a jumping spider, *Pellenes* sp.) was rare that year, causing the advantage that membracids derived from ant attention to be either absent or so small as to be unmeasurable. Furthermore, the need for protection depended on a membracid's life-history stage. In years in which a benefit could be documented, nymphs survived about 56% better in the presence of ants, whereas survival of adults was unaffected. This result is also probably related to the impact of predators. Adult membracids possess heavily sclerotized exoskeletons and are highly mobile, and are thus well-protected even in the absence of ant defenders. In contrast, nymphs are soft-bodied, relatively sedentary and hence more vulnerable to predation.

Costs and benefits in this mutualism also vary over space. Ants are understandably more attracted to larger membracid aggregations, which provide more food for them. The consequence for membracids is a 40% increase in survivorship when they occur in a large group[15]. Further experiments by Cushman and Whitham[26] have shown that when neighboring aggregations compete for the attention of ants, per-capita protection is reduced significantly. Spider predation increases as a result, in part because spiders choose to forage where the aggressive ants are rare.

Thus, the outcome of this interaction is sensitive to three kinds of variability[14]: variation in the ecological problems that membracids experience (i.e. spatial and temporal shifts in predator abundance); variation in the benefit that their ant mutualists are able to provide (predator protection, but only for certain life-history stages and only when predators are abundant); and variation in the availability of mutualists (related in this case to the size and number of membracid aggregations competing for attention).

Where to expect conditionality

Conditional outcomes have now been documented in nearly every kind of species interaction, not only within mutualisms[6,14,27,28]. Furthermore, they have been noted for every form of mutualism studied to date, ranging from

symbioses[19,20,29] to looser interactions involving free-living partners, and encompassing mutualisms with widely divergent rewards and services. Are conditional outcomes equally likely across all interactions, or are there predictable patterns to their occurrence? As a start towards answering this question, I will suggest three as-yet untested predictions regarding where outcomes of mutualisms are likely to vary the most.

Prediction 1: Outcomes of facultative mutualisms should be more variable than outcomes of more obligate mutualisms

Obligate mutualists cannot survive for long without each other; any reduction in the abundance or quality of service of one mutualist is likely to feed back immediately and strongly to the fitness of its partner. It is reasonable to suspect that traits buffering obligate interactions from environmental variability have been strongly selected. For example, the risks of establishing in a habitat with few or no mutualists are minimized in certain specialized associations by adaptations for joint dispersal or direct transfer of mutualists from parent to offspring[30]. In contrast, in looser, less-specific associations, decreased abundance of one mutualist is often accompanied by an increased presence of alternative, acceptable mutualist species[31,32]. Furthermore, many facultative mutualists are able to survive and reproduce to some extent even in the total absence of the reward or service provided by their partners. For example, plants protected by facultative ant defenders (Box 3) usually survive herbivore attack when ants are absent; the ants, in turn, have broad diets and are not closely dependent upon plant-produced food rewards. Ecological variability and, thus, conditional outcomes of mutualism should therefore carry less-extreme fitness costs in less-obligate interactions.

Prediction 2: Mutualisms in which a third species is intimately involved are more likely to show conditional outcomes than are other forms of mutualism

The service provided in many mutualisms is protection from natural enemies (Box 3). As seen in the ant/membracid mutualism studied by Cushman and Whitham[15,26], outcomes of such interactions are affected not only by factors that affect the abundance and behavior of the mutualists themselves, but by variations in the abundance, behavior and identity of their enemies (i.e. the 'ecological problem' at hand[3,14]). Additionally, the outcome of mutualisms in which one partner is the antagonist of a third species is known to be directly and strongly affected by the identity and health of that species[16]. These mutualisms, therefore, should be those most sensitive to variation in the biotic environment in which the interaction takes place.

Prediction 3: Mutualisms in which benefits are functions of the abundance of partners will show greater conditionality than those in which a single individual can satisfy the requirement for reward or service

Small changes in population sizes can easily shift outcomes in some mutualisms[3]. In most plant species, for example, pollen delivery and dispersal are functions of the number of pollinator visits per flower, which are highly variable in space and time[10]. However, certain plants, including many orchids, require only a single visit per flower to achieve maximal pollen removal and delivery. We could predict that on a per-plant basis, such species experience less variable (although not necessarily higher average) reproductive success.

These predictions may illuminate why conditionality has been so commonly noted in mutualisms in which ants defend reward-producing insects or plants (Box 3). These interactions are rarely obligate (Prediction 1). Their costs and benefits shift with the identity and abundance of other associates (Prediction 2): herbivores, in the case of ant–plant mutualisms, and predators and host plants, in the case of ant–herbivore mutualisms. Finally, ants exhibit density-dependent recruitment to food sources[33], increasing the likelihood that per-capita costs and benefits will be shifted with population sizes of ants and their mutualists (Prediction 3).

Evolutionary significance of conditional outcomes

Conditionality is more than a purely ecological phenomenon. Although its evolutionary significance is, as yet, largely unexplored, we can predict that conditionality should directly influence the ways in which interactions evolve[6,14,16]. The strength of natural selection within a mutualism should be related to the magnitude of the net benefits, that is, to the size of the 'pluses' on the part of the interaction continuum that it occupies (Box 2). Temporal variation in net benefits should affect the rate of evolutionary change within the mutualism, while spatial variation could (depending on the rate of gene flow) result in geographical differences in the degree of mutual dependency that evolves. Furthermore, outcomes of many interactions shift not only in magnitude but in direction or sign with the ecological setting[16]. For example, Maschinski and Whitham[34] have shown that net effects of herbivory on *Ipomopsis aggregata* range from strongly negative to weakly positive along a gradient of nutrient availability; similarly, under specific conditions, ants will devour rather than protect their homopteran associates[16,33]. It is essential to determine the range of natural ecological conditions known to influence the relative and absolute magnitudes of costs and benefits, if we want to predict whether adaptations promoting mutualism or antagonism (or both!) are likely to evolve in a given interaction.

Conclusion

The history of mutualism studies has been marked by a series of debates about whether certain associations are or are not mutualistic (e.g. the recent controversy on possible benefits of herbivory to plants[34-36]). These disagreements have often originated from an initial assumption that a given interaction has a single anticipated outcome, consistent with the typology of the 'interaction grid' (Box 2). In contrast, viewing interactions as a continuum leads us to expect a range of outcomes (some certainly more likely than others), many of them contingent upon mutualists' life-history stage, population size and current ecological setting[35,36]. Although evidence for conditionality is abundant in the ecological literature, we are only beginning to develop a complete picture of its scope and significance for single interactions. Studies of these phenomena should shed new light on both the ecological and evolutionary dynamics of interspecific relationships.

References
1 Boucher, D.H., James, S. and Keeler, K.H. (1982) *Annu. Rev. Ecol. Syst.* 18, 315–347
2 Boucher, D.H., ed. (1985) *The Biology of Mutualism*, Croom Helm
3 Addicott, J.F. (1984) in *A New Ecology* (Price, P.W., Slobodchikoff, C.N. and Gaud, B.S., eds), pp. 437–455, Wiley and Sons
4 Addicott, J.F. (1985) in *Community Ecology* (Case, T. and Diamond, J., eds), pp. 425–436, University of California Press
5 Thompson, J.N. (1982) *Interaction and Coevolution*, Wiley and Sons
6 Thompson, J.N. (1988) *Annu. Rev. Ecol. Syst.* 23, 65–87
7 Cushman, J.H. and Beattie, A.J. (1991) *Trends Ecol. Evol.* 7, 193–195
8 Bronstein, J.L. (1994) *Q. Rev. Biol.* 69, 31–51
9 Southwick, E.E. (1984) *Ecology* 65, 1775–1779
10 Bronstein, J.L. in *Mosaic Landscapes and Ecological Processes* (Fahrig, L., Hansson, L. and Merriam, G., eds), Chapman and Hall (in press)
11 Yamamura, N. (1993) *Theor. Pop. Biol.* 44, 95–109
12 Freeman, S. and Rodriguez, R.J. (1993) *Science* 260, 75–78
13 Bull, J.J. and Molineux, I.J. (1992) *Evolution* 46, 882–895
14 Cushman, J.H. and Addicott, J.F. (1991) in *Ant–Plant Interactions* (Huxley, C.R. and Cutler, D.F., eds), pp. 92–103, Oxford University Press
15 Cushman, J.H. and Whitham, T.G. (1989) *Ecology* 70, 1040–1047
16 Cushman, J.H. (1991) *Oikos* 61, 138–144
17 O'Dowd, D.J. (1979) *Oecologia* 43, 233–248
18 Wyatt, R., Broyles, S.B. and Derda, G.S. (1992) *Am. J. Bot.* 79, 636–642
19 Bowen, G.D. (1980) in *Tropical Mycorrhizal Research* (Mikola, P., ed.), pp. 116–190, Clarendon Press
20 Akkermans, A., Hahn, D. and Zoon, F. (1989) *Ann. Sci. For. (Supplement)* 46, 765–771
21 Breton, L.M. and Addicott, J.F. (1992) *Oikos* 63, 253–259
22 Losey, G.S. (1972) *Copeia* 1972, 820–833
23 Gorlick, D.L., Atkins, P.D. and Losey, G.S. (1978) *Am. Nat.* 112, 341–353
24 Breton, L.M. and Addicott, J.F. (1992) *Ecology* 73, 2175–2180
25 Falkowski, P.G., Dubinsky, Z., Muscatine, L. and McCloskey, L. (1993) *BioScience* 43, 606–611
26 Cushman, J.H. and Whitham, T.G. (1991) *Am. Nat.* 138, 851–865
27 Dunson, W.A. and Travis, J. (1991) *Am. Nat.* 138, 1067–1091
28 Michalakis, Y., Olivieri, I., Reynaud, F. and Raymond, M. (1992) *Trends Ecol. Evol.* 8, 59–62
29 Saffo, M.B. (1992) *Symbiosis* 19, 16–34
30 Smith, D.C. and Douglas, A.E. (1987) *The Biology of Symbiosis*, Edward Arnold
31 Howe, H.F. (1984) *Am. Nat.* 123, 764–777
32 Davidson, D.W., Snelling, R.R. and Longino, J.T. (1989) *Biotropica* 21, 64–73
33 Beattie, A.J. (1985) *The Evolutionary Ecology of Ant–Plant Mutualisms*, Cambridge University Press
34 Maschinski, J. and Whitham, T.G. (1989) *Am. Nat.* 134, 1–23
35 Paige, K.N. and Whitham, T.G. (1987) *Am. Nat.* 129, 407–416
36 Bergelson, J. and Crawley, M.J. (1992) *Am. Nat.* 139, 870–882
37 Lewis, D.H. (1985) in *The Biology of Mutualism* (Boucher, D.H., ed.), pp. 30–39, Croom Helm
38 de Bary, A. (1879) *Die Erscheinung der Symbiose*, Karl J. Trübner
39 Abrams, P.A. (1987) *Oecologia* 73, 272–281