

---

# From mutualism to antagonism: the coevolutionary influence of context-dependent interactions in mutualistic networks

---

Lucas A. Camacho<sup>1</sup> and Paulo Roberto Guimarães Junior<sup>2</sup>

<sup>1,2</sup>Departamento de Ecologia, Universidade de São Paulo, Rua do Matão, travessa 14, nº 321, Cidade Universitária, São Paulo - SP, CEP: 05508-090, Brasil.

## 1 Introduction

1 Coevolution, the reciprocal evolutionary change between interacting species, is a main  
2 force influencing the diversity of species and the organization of ecological interactions  
3 in the community. The interactions structure (who interacts with whom) dictates which  
4 species are coevolving in the community. Thus, coevolution is a process that molds and is  
5 molded by ecological interactions. The most conspicuous known patterns of coevolution  
6 are on species traits related to ecological interactions like plants and herbivores, pollination  
7 or seed dispersal.

8 Historically, the empirical evidences of coevolution thrilled several worldwide known  
9 naturalists to describe the genetic and ecological mechanisms that fuel coevolution and,  
10 consequently, influences the ecological interactions between species in communities. Daniel  
11 Janzen described a high specialized mutualistic interaction formed by coevolution between  
12 the acacia ant (*Pseudomyrmex ferruginea*) and the bullhorn acacia (*Acacia cornigera*). In  
13 this system, the ant lives exclusively in structures produced by the plant called domatia

14 and repeal possible herbivores that may attack the plants. In this way, the ant has his  
15 colony guaranteed and the plant repeal unwanted visitors. Also, Fritz Müller studied the  
16 coloration patterns of neotropical butterflies and propose the first mathematical model to  
17 show how these patterns emerge in this butterflies by coevolution.

18 Systems of coevolution between two species grounded the studies of how several species  
19 can coevolve in nature. Several species implies in several reciprocal evolutionary changes  
20 happening at the same time. Thus, coevolution process depends on how the ecological  
21 interactions are distributed in the community. A problem that emerge is how to account  
22 several reciprocal evolutionary changes at once. An possible approach to solve this issue is  
23 use network theory. Networks are representations of species and the interactions between  
24 these species in the community. The use of networks of interactions enable the investi-  
25 gation of how different evolutive process form phenotypic pattern of species. Using the  
26 networks approach, we now know that coevolution in mutualistic networks of interactions  
27 lead to trait complementarity of species that interact. In antagonisms otherwise, the se-  
28 lection intensity acting on a prey and the predator can create coevolutionary arm's race.  
29 This different coevolutionary dynamics can reorganize the interactions structure in time,  
30 generating for example, temporal variation in species traits between interacting species.

31 The species traits that will be favoured by natural selection, the interaction network  
32 structure and the path of the coevolution process rely on the costs and benefits associated  
33 with different interaction outcomes. For example, mutualisms shows a higher benefit  
34 compared to the cost for both interacting species. If so, the efficiency of interaction will  
35 be higher in species with similar traits, where the species that has the higher proportion  
36 of interactions will order the trait complementarity generating a particular coevolution  
37 process. Else, antagonism interactions shows a higher benefit than the cost for a predator

38 or parasite and a low benefit than the cost for the prey or host. Considering now an  
39 antagonism network of interactions, explorer species that has explored species similar  
40 traits will be favoured. Otherwise, the higher explored trait difference than the explorer,  
41 better for the explored species, generating an arm's race coevolution dynamics. Despite  
42 the actual knowing of how these interaction outcomes will influence coevolution, there is  
43 a lack of knowledge on how these two outcomes in the same network can influence the  
44 coevolution process and the structure of interaction in the community.

45 Despite the utility of classifying the interactions by their costs and benefits, these costs  
46 and benefits are not fixed. In fact, there is growing evidence quantifying the outcomes  
47 variation of interactions in space and time. In the ant-plant system exemplified, a low  
48 abundance of acacia ants caused by external factors of the plant (*i.e.* temperature, rain-  
49 fall) can cause a low herbivore reaping efficiency. In this scenario, is possible that the  
50 production cost of domatia for the plant could be higher than the benefits from the ants.  
51 In this way, this interaction between the plant and the ant can pass from a mutualism to  
52 an antagonism, which the ant is benefited and the plant suffers from a higher cost. The  
53 interactions outcomes which vary in space or time because of biotic and abiotic factors  
54 are called context-dependent interactions.

55 The shift in interaction outcomes between mutualism and antagonism caused by the  
56 context-dependency creates networks that has bot antagonism and mutualism outcomes  
57 together. Considering that the trait changing path of these two dynamics are pretty  
58 different, the coevolutionary dynamics will be favoured by these two types of interactions.  
59 More than that, the interactions outcomes varying in time in the same community can  
60 influence species more in a mutualism or antagonism-like dynamic, depending on the  
61 network structure of interactions and how these outcomes shifts happen in time. In

62 other words, the context dependency of interactions changing the interactions outcomes  
63 generates changes in the coevolutionary dynamics of species, contributing to the trait  
64 diversity of species and interaction structure of the community. Thus, the presence of  
65 different outcomes and context-dependent interactions should not be ignored if we want  
66 a higher understanding of the ecosystems function and diversity.

67 Here, we use a single trait mathematical model, theoretical and empirical networks  
68 of species interactions and computer simulations to fill the gap of merge two different  
69 interaction outcomes in one network of interactions and consider the context-dependency  
70 of these interactions outcomes. Specifically, we are trying to answer two mais questions:  
71 *i)* how changes the structure of networks of interactions with both antagonism and mu-  
72 tualism together? *ii)* how context-dependent interactions influences the coevolutionary  
73 process?

## 2 References

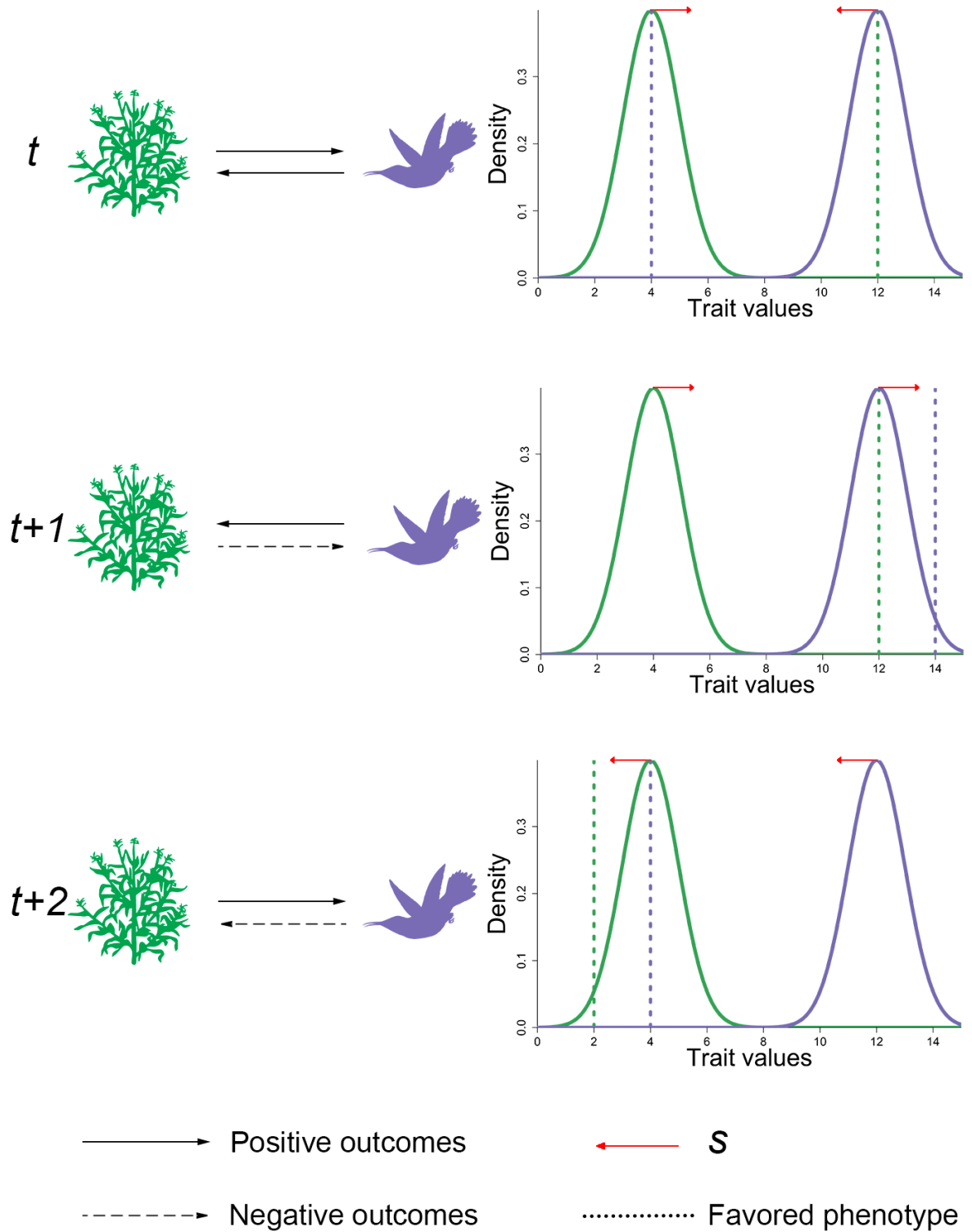


Figure 1: Conceptual figure showing the interaction outcomes changing from a mutualism ( $t$ ) to an antagonism with different outcome arrangements ( $t+1$  and  $t+2$ ). There are different favoured phenotypes and selection differentials ( $s$ ) depending on how the interaction outcomes are arranged. The mutualism promotes trait matching and the antagonism promotes arm's race between the explorer and exploited species.