From friend to foe and back - Coevolutionary transitions in the mutualism-antagonism continuum

Abstract

Interspecific interactions evolve along a continuum ranging from mutualism to antagonism. Evolutionary theory so far focused mostly on parts of this continuum, notably on mechanisms that enable and stabilise mutualism. These mechanisms often involve partner discrimination ensuring that interaction intensity is higher with more cooperative partners. However, the gradual trajectory of coevolutionary transitions between mutualism and antagonism remains unclear. Here, we model how discrimination ability in one partner coevolves with cooperativeness in the other and analyse the resulting evolutionary trajectories in the mutualism-antagonism continuum. We show that strong ecological change, such as a radical host shift or colonisation of a new environment, can trigger transitions in both directions including back-and-forth transitions between antagonism and mutualism. Moreover, we find an evolutionary tipping point: a stable mutualism may break down to antagonism if the cost of either mutualistic service or discrimination ability gradually increases above a threshold beyond which this transition cannot be reversed by reducing costs again. Our study provides a new perspective on the evolution of biotic interactions and hence on the dynamic structure of ecological networks.

Keywords

biotic interactions, coevolution, evolutionary transitions, theoretical ecology, evolution of mutualism, critical transition

1 Introduction

Interspecific interactions play a key role for ecological and evolutionary dynamics. They can be classified into different interaction types, according to the effect on the fitness of the two involved partners. For instance, antagonism exists in host-parasite relationships, whereas plant-pollinator interactions are an important example for mutualism. However, mutualism and antagonism are not unbridgeable opposites but rather span a continuum with any gradation possible [1, 2]. An interaction's location in this continuum is by no means fixed. Apart from environmental variation and intraspecific heterogeneity, also evolution changes the costs and benefits for both interaction partners and thereby moves the interaction across the continuum [3, 4]. Eventually, this can result in evolutionary transitions from mutualism to antagonism or vice versa [1, 5].

For example, lineages of originally mutualistic yucca moths evolved into antagonists that stopped pollinating yucca plants but continued ovipositing in the ovary of the flower where the larvae feed on developing seeds [6, 7]. Vice versa, there is compelling evidence of microbial parasites evolving to reduce their virulence, ultimately becoming mutualists [5, 8, 9]. Such shifts of interaction type can have major consequences for community dynamics, ecosystem services or human health [5, 10, 11], and are hypothesised to underlie major evolutionary innovations such as the evolution of pollination [12, 13]. However, a comprehensive theoretical understanding of the gradual evolution of interaction types is still missing [8, 10, 14].

Theoretical work has looked at evolutionary transitions of interaction type mainly through the lens of the classic question: 'How can mutualism evolve and how can it be maintained in the face of cheaters?' [15, 16, 17, 18, 19, 20]. While several mechanisms have been identified that potentially enable the evolution of mutualism from antagonism [7, 21, 22, 23], the specific coevolutionary trajectory in the mutualism-antagonism continuum has received little attention. Many models in this context, in particular game-theoretical ones, interpret cooperation and defection as two discrete strategies, ignoring the continuum between them [22, 24, 25, 26, 27, 28]. Studies that instead model the evolution of quantitative traits influencing the interaction type usually do not quantify the precise border between antagonism and mutualism, making it hard to derive conclusions about the course of the transition [29, 30, 31; but see 32].

The focus on the evolution of mutualism introduces a bias in the literature with respect to the direction of transition: very few studies examine the evolutionary shift from mutualism to antagonism [10, 33; but see 34]. Although some empirical results suggest that this occurs less frequently than the transition from antagonism to mutualism [5, 8, 35], inclusion of both transition directions is needed for a comprehensive understanding of dynamics in the mutualism-antagonism continuum, also accounting for reversibility of transitions. This holds especially in times of rapid environmental change which triggers diverse coevolutionary adaptations by altering the costs and benefits of an interaction. The resulting potential for mutualism breakdown is a threat for numerous ecosystem services [10].

Here, we present a general model of gradual evolutionary transitions from antagonism to mutualism and vice versa. We track the location of an interaction in the continuum through time. The structure of our model reflects the asymmetry often observed in empirical systems: One partner can potentially transition between antagonist and mutualist by adapting its degree of cooperativeness while the other is able to evolve some discrimination ability, that is, the ability to adapt the strength of interaction according to the cooperativeness of the partner [36, 37]. This comprises different mechanisms thought to promote the evolutionary emergence of mutualism. For instance, partner choice, where one partner can choose beforehand with whom it interacts [15, 19, 38], can be interpreted as conditional adaptation of interaction probability or frequency. Sanctions, where one partner may punish bad-quality partners after engaging in the interaction [39, 40], correspond to a response of interaction duration or intensity to varying cooperativeness.

We use the model to identify pathways of gradual evolutionary transitions of interaction type. In particular, we first analyse the transient coevolutionary dynamics with different initial trait values and examine the effect of varying relative speed of evolution, known to significantly influence any coevolutionary process [41, 42, 43, 44]. In a second step, we then study how varying environmental conditions in the form of varying cost and benefit parameters affects the possibility and course of transitions. We find potential for transitions in both directions as well as back-and-forth transitions, mainly dependent on preadaptation in discrimination ability.

Moreover, we observe an evolutionary tipping point: When costs of mutualism or discrimination ability gradually exceed a threshold due to environmental change, a stable mutualism abruptly evolves towards antagonism, with limited reversibility. Our model thus yields qualitatively new results on coevolutionary dynamics in the mutualism-antagonism continuum.

2 Model and Methods

2.1 Cooperativeness and discrimination ability

We model a system consisting of two interacting species called 'host' and 'partner'. While the fitness effect of the interaction for the partner is always positive, the host may either benefit or suffer from the interaction, representing mutualism or antagonism, respectively. By explicitly quantifying the fitness effect of the interaction for both host and partner, we are able to track the position of the interaction in the mutualism-antagonism continuum. This includes the special case of commensalism, where the interaction has no effect on host fitness. We assume that the location of the interaction in the continuum is solely determined by traits of the two involved species. Thus, we restrict ourselves to investigate transitions of interaction type resulting from evolutionary adaptation as opposed to transitions due to changing exogeneous biotic or abiotic conditions in context-dependent interactions.

As an example, throughout this section we refer to the nutrient exchange symbiosis between a legume host and a rhizobium. Rhizobia are soil bacteria that infect the roots of legumes where they fix nitrogen (N) from the atmosphere and release it to the plant, while receiving carbon in return. Depending on the level of N they fix, rhizobia can range from mutualists to antagonists [45]. Note, however, that the applicability of the model is neither limited to plant-microbe interactions, nor to actual symbioses.

We focus on two key phenotypic traits that coevolve. The partner has a trait β representing its cooperativeness, that is, the service it provides to the host. β can be positive or negative, indicating mutualism or antagonism, respectively. In the legume-rhizobium interaction, this corresponds to the level of N fixation of the bacterium with negative values representing levels lower than what is needed to cover the costs of the plant. The host has a trait $\alpha \geq 0$ representing its discrimination ability. α measures the extent to which the interaction strength depends on the partner's cooperativeness (see Fig. 1). If $\alpha = 0$ (no discrimination ability), interaction strength is independent of whether the partner is beneficial or detrimental for the host. If α is instead large, the interaction strength $S(\alpha, \beta)$ highly depends on the partner trait: $S(\alpha, \beta)$ is close to 0 in case

of an antagonistic partner (representing avoidance of the interaction) and approximates 1 for a highly mutualistic partner. This relation is mathematically expressed using a sigmoid function:

$$S(\alpha, \beta) = \frac{1}{1 + e^{-\alpha\beta}} \tag{1}$$

In the legume-rhizobium interaction, α represents the accuracy with which the legume directs carbon to mutualistic as opposed to non-mutualistic rhizobia.

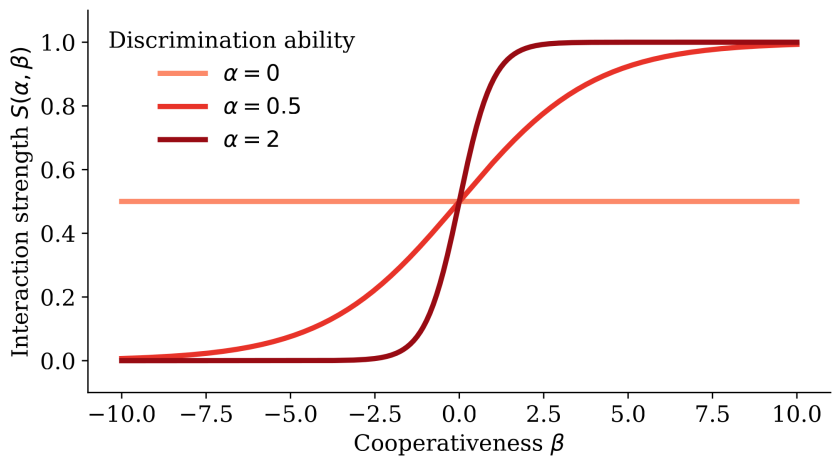

Figure 1: **Dependence of interaction strength on discrimination ability of the host and cooperativeness of the partner.** For small discrimination ability α, the influence of cooperativeness β on the interaction strength is negligible. For higher α, interaction strength is high with mutualistic partners, but low with antagonistic ones.

2.2 Fitness effects of the interaction

The following equations describe the fitness effects of the interaction on the host (w_H) and its partner (w_P), that is, the increase or decrease in per-capita fitness due to presence of the other species. Note that we decided to use a model without explicit population dynamics (see Supplementary Material S.1 for justification).

$$\begin{aligned} w_H &= S(\alpha, \beta)\beta - c_\alpha \alpha \\ w_P &= S(\alpha, \beta)(b - c_\beta \beta) \end{aligned} \tag{2}$$

The fitness effect on the host w_H is given by the cooperativeness β of the partner multiplied with the interaction strength $S(\alpha, \beta)$, which depends on both host discrimination ability and partner

phenotype as outlined above. Host discrimination ability comes at a cost for the host that is proportional to α with cost factor c_α (cost of discrimination ability). For example, this could be an energetic cost for processing the signal about the N fixation level in the molecular dialogue between legume and rhizobium. Note that this cost term is not multiplied with the interaction strength, so that it is paid regardless of how frequent or how likely the interaction is.

The effect of the interaction on the partner fitness w_P is given by a positive baseline benefit b that is reduced by the product of cooperativeness β and cost factor c_β (cost of mutualism). This reflects the principal assumption that providing a mutualistic service is costly, posing a fundamental conflict of interest between the two species. Although empirical evidence is not unambiguous [16, 46], this is likely to hold in many systems and is the basis for the majority of theoretical research in this context to date [7, 22, 28, 30, 36]. In the legume-rhizobium example, c_β corresponds to the costs of N fixation. The cost of mutualism scales with interaction strength, so that it is paid more often when the interaction is more frequent or more intense.

2.3 Evolutionary dynamics

The simultaneous changes in mean trait value of both discrimination ability α and cooperativeness β are described by differential equations:

$$\begin{aligned} \frac{d\alpha}{dt} &= v_H \cdot \underbrace{\left.\frac{\partial w_H(\alpha', \beta)}{\partial \alpha'}\right|_{\alpha'=\alpha}}_{\text{host selection gradient}} \\ \frac{d\beta}{dt} &= v_P \cdot \underbrace{\left.\frac{\partial w_P(\alpha, \beta')}{\partial \beta'}\right|_{\beta'=\beta}}_{\text{partner selection gradient}} \end{aligned} \tag{3}$$

These equations arise from quantitative genetics under the assumption of small trait variance [47, 48, 49] and resemble the Canonical Equation of adaptive dynamics [50]. Trait change is proportional to the selection gradient, the local gradient of the fitness function with respect to the focal trait. v_H and v_P are the additive genetic variances for the host and partner trait divided by the respective generation time [43]. They represent the speed of evolutionary adaptation in host and partner, assumed to be constant over time, and influenced by rate and effect size of

mutations. To prevent biologically implausible negative values of discrimination ability α, we set $\frac{d\alpha}{dt} = 0$ in case of $\alpha = 0$ and a negative host selection gradient.

Note that we assume that only the per-capita fitness effects of the interaction w_H and w_P determine selection in our model. We thereby neglect the influence of other selection pressures on the focal traits as well as potential density-dependent selection (see Supplementary Material S.1 for alternative model formulations).

Table 1: Model parameters and their standard values.

Parameter	Meaning	Standard value
b	basic benefit for partner	1
c_α	cost of discrimination ability	0.1
c_β	cost of mutualistic service	0.2
v_H	speed of host adaptation	0.02
v_P	speed of partner adaptation	0.02

2.4 Model analysis

First, we analyse the evolutionary dynamics in the model using the baseline parameterisation given in Table 1. We start by examining the sign of the selection gradients for host and partner (see equations 3) depending on discrimination ability α and cooperativeness β. In particular, we focus on the shape of the evolutionary null-isoclines where the host or partner selection gradient equals zero. The intersections of host and partner null-isocline represent evolutionary fixed points which are potential endpoints of evolution since selection pressures vanish for both species. Using the eigenvalues of the Jacobian of the system described by equations 3, we assess the local asymptotic stability of the fixed points, i.e. whether evolution will let a system close to a fixed point converge to it or not.

The insights gained into the system's behaviour subsequently enable us to understand the evolutionary transitions from antagonism to mutualism and vice versa in the transient dynamics

of the model (i.e. when starting far from an evolutionary equilibrium). We compare the potential for evolutionary transitions in the transient dynamics for varying relative speed of evolution, mediated by a varying ratio of v_H and v_P.

Finally, we aim at identifying potential evolutionary transitions resulting from gradual change in the biotic and abiotic environment. We interpret environmental change implicitly as a modification of the cost and benefit parameters c_α, c_β and b. For instance, in the legume-rhizobium interaction, a long-term nitrogen enrichment of the soil would correspond to an increase of costs for the rhizobium for providing the same fitness benefit to the plant, since the plant can use soil N more easily.

The outlined analyses already account for variation of any model parameter which ensures the generality of the obtained results (see Supplementary Material S.1).

2.5 Individual-based simulations

We complement the outlined model by individual-based simulations that relax some of the strict assumptions of the analytical approach (see Supplementary Material S.2). In particular, we introduce demographic stochasticity and intraspecific variation, as well as the possibility of large-effect mutations to the system. Each of these aspects can potentially alter the evolutionary dynamics fundamentally [41, 51, 52, 53]. Notably, the individual-based model allows for comparison of scenarios with varying effect size of mutations. The implementation is closely oriented to the analytical model in order to ensure comparability.

3 Results

3.1 Two evolutionary attractors

We first examine the sign of the two selection gradients and the shape of the evolutionary null-isoclines. This enables us to understand the selection mechanisms that underlie potential transitions in the mutualism-antagonism continuum in the model. Figure 2a shows the sign of the selection gradient for the partner cooperativeness β depending on host discrimination ability α and β. A positive selection gradient means selection for increased mutualism, a negative selection gradient represents selection for more antagonistic values of β. Without any discrimination by the host ($\alpha = 0$), selection is always negative due to the cost of mutualism. However, with increased discrimination ability, the partner experiences selection for higher values of β in order to prevent being rejected by the host. The border between the region of positive and negative selection is the evolutionary null-isocline for the partner. It can be shown that the partner null-isocline crosses the x-axis at $\alpha = 2c_M/b$ (see Supplementary Material S.3). This means that a partner interacting with a non-evolving host becomes a mutualist if and only if the host's discrimination ability exceeds twice the costs of mutualistic engagement divided by the basic benefit for the partner. Note that for very high values of discrimination ability α it suffices for the partner to be only slightly mutualistic to retain full interaction strength by the host (see Fig. 1). Therefore, as stronger mutualism is costly, the partner null-isocline approximates commensalism ($\beta = 0$).

Next, we look at the selection gradient for the discrimination ability of the host α and the corresponding evolutionary host null-isocline (Fig. 2b). For $\beta = 0$, the interaction does not affect host fitness, hence there is no need to invest in discrimination: Selection is always negative. However, if the cooperativeness of the partner β is positive or negative enough, a certain degree of discrimination becomes worthwhile. This either reflects selection for increasing interaction strength with a mutualist (region of positive selection above x-axis) or selection for avoidance of an antagonist (region of positive selection below x-axis). For very high or very low values of β, already a slight investment in discrimination ability renders the discrimination almost maximally efficient, as can be seen from the shape of the interaction strength function S (see Fig. 1). Therefore, the host null-isocline approaches the y-axis (no discrimination) asymptotically.

We find three evolutionary fixed points at the intersections of the null-isoclines in the trait space (the space spanned by the traits α and β), as shown in Fig. 2c. A linear stability analysis using the eigenvalues of the Jacobian of the system reveals that two of them are locally asymptotically stable (indicated by yellow dots), meaning that evolutionary trajectories starting nearby eventually end up at the fixed point. This is confirmed by numerical simulations of the coevolutionary dynamics for varying initial combinations of host discrimination ability and partner cooperativeness, the trajectories of which are plotted in Fig. 2c. One of the two attractors is located in the antagonistic region ($\beta < 0$) at a low value of α while the other is a mutualistic attractor ($\beta > 0$) with a considerably higher discrimination ability of the host. Additionally, there is an unstable mutualistic fixed point (indicated by a white dot).

The eigenvalues at the antagonistic attractor have a non-zero imaginary part ($-3.5 \cdot 10^{-4} + 6 \cdot 10^{-3} i$ and $-3.5 \cdot 10^{-4} - 6 \cdot 10^{-3} i$). This is consistent with the fact that evolutionary trajectories approaching this fixed point show oscillatory behaviour: Increased discrimination ability selects for higher cooperativeness, which in turn selects for lower discrimination ability since discrimination is not needed when the interaction approaches commensalism. Lack of discrimination selects for antagonistic behaviour of the partner, putting positive selection pressure on discrimination ability again and the loop starts all over. By contrast, the eigenvalues at the mutualistic attractor are real numbers ($-1.7 \cdot 10^{-3}$ and $-6.9 \cdot 10^{-3}$), indicating non-oscillatory trajectories close to this attractor.

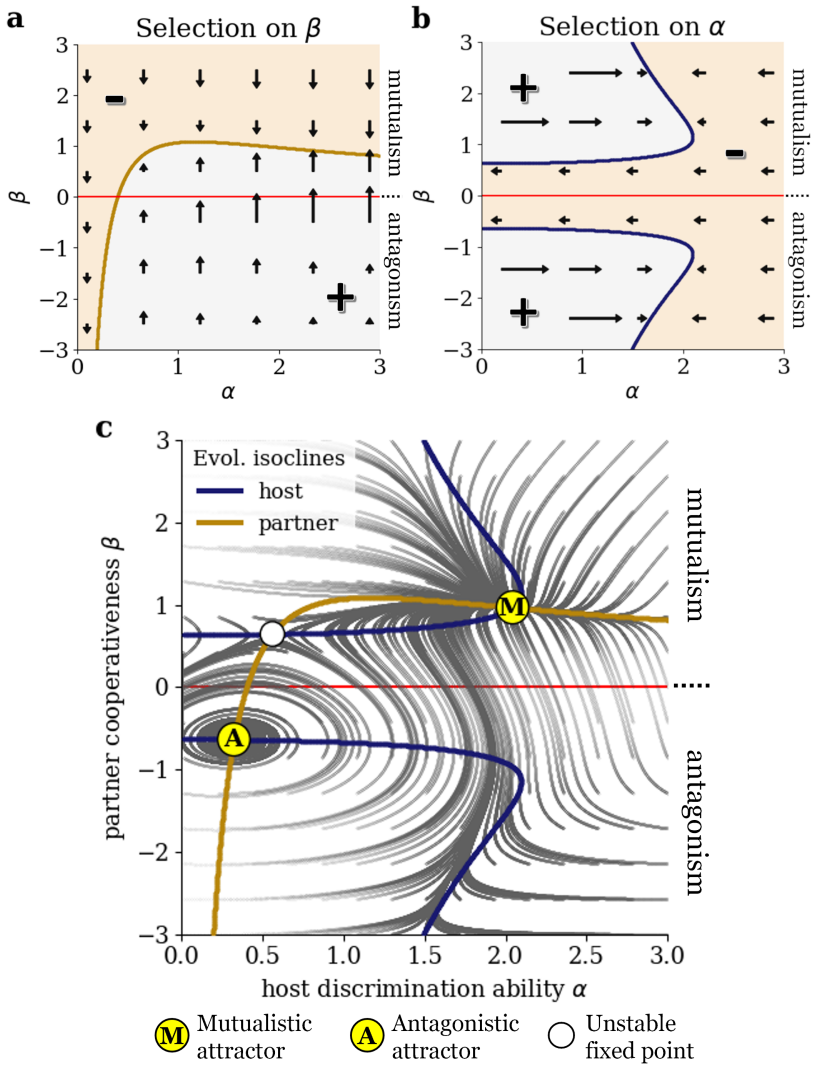

Figure 2: **Coevolution of cooperativeness and discrimination ability along the mutualism-antagonism continuum.** Colour plots show the sign of the selection gradients for (**a**) the partner cooperativeness β and (**b**) the host discrimination ability α, depending on α and β (all other parameters are chosen according to Table 1). Positive selection gradient is shown in light grey, light brown colour indicates negative selection gradient. Arrows visualise the direction and strength of selection. The blue and brown line represent host and partner evolutionary null-isocline, respectively, where selection on α or β vanishes. (**c**) The intersections of the null-isoclines are the stable/unstable evolutionary fixed points, marked by yellow/white circles. The dark grey lines visualise the evolutionary trajectories for varying initial values of discrimination ability α and cooperativeness β.

3.2 Relative speed of evolution governs transitions of interaction type

We closer examine the potential for evolutionary transitions along the mutualism-antagonism continuum in the transient dynamics of the system and compare scenarios with varying relative speed of evolution v_H/v_P. The adaptation speeds do not change the sign of the selection gradients and consequently have no effect on evolutionary null-isoclines and location of evolutionary fixed points in the trait space. However, the ratio v_H/v_P alters the shape of the trajectories leading to the evolutionary attractors. The evolutionary trajectories for varying relative speed of evolution are shown in Figure 3. Trajectories are coloured blue if they converge to the mutualistic attractor and red if they end up at the antagonist attractor, visualising the basins of attraction, that is, the set of initial conditions for which the system converges to a given fixed point. A transition from mutualism to antagonism or vice versa corresponds to a change of sign of β, i.e. a crossing of the x-axis.

In general, there are three different pathways for evolutionary transitions from antagonism to mutualism or vice versa (see highlighted trajectories in Fig. 3):

1. An initially mutualistic partner becomes antagonistic because of the host's low initial discrimination ability.

2. An initially antagonistic partner becomes mutualistic because of the host's high initial or evolved discrimination ability.

3. An initially antagonistic partner first becomes mutualistic due to initial or evolved discrimination ability, but not mutualistic enough to prevent further evolution of reduced discrimination ability; the partner finally becomes antagonistic again (back-and-forth-transition).

For a fast evolving partner ($v_H/v_P = 0.1$, see Fig. 3a), the outcome of the evolution strongly depends on the initial discrimination ability of the host. If α is low, the partner will quickly evolve antagonist behaviour and the system ends up at the antagonistic attractor. In particular, high speed of partner evolution increases the occurrence of transitions from mutualism to antagonism. However, if there is enough preadaptation in discrimination ability ($\alpha \gtrsim 0.6$), there is selection for the partner to exhibit more mutualistic behaviour and trajectories end up at the

mutualistic attractor (potential for transitions from antagonism to mutualism). There is only a small window of initial conditions allowing for a back-and-forth transition.

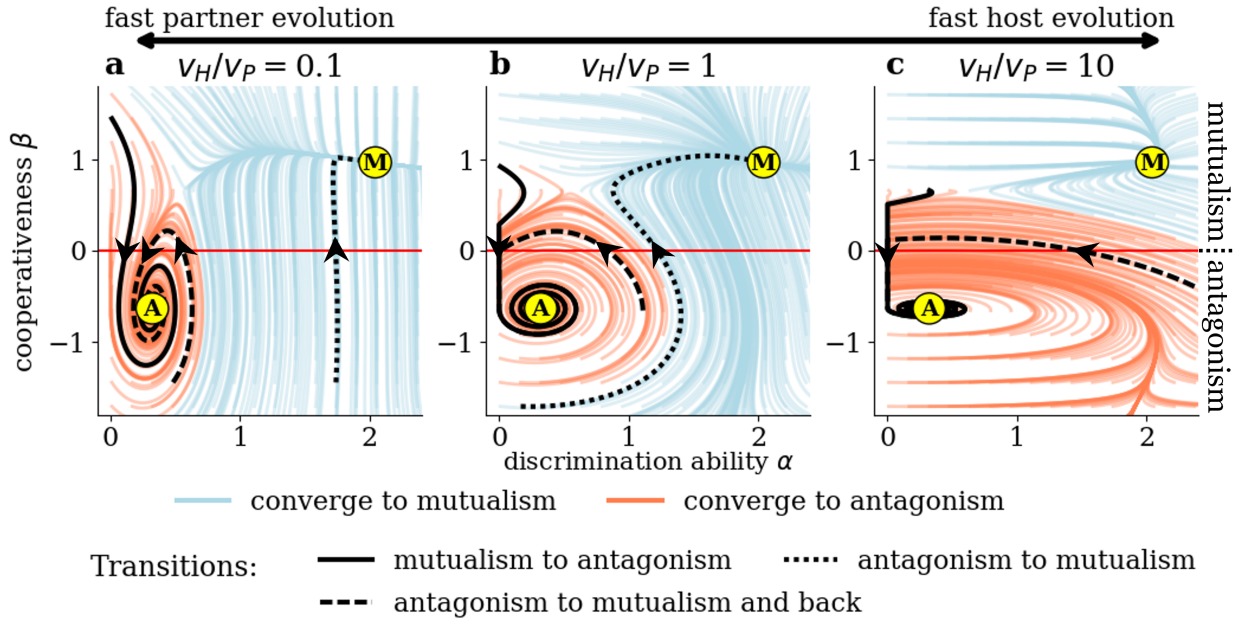

Figure 3: **Evolutionary transitions between mutualism and antagonism depend on the relative speed of evolution in hosts and partners.** Evolutionary trajectories are shown for (a) fast partner evolution, (b) comparable speed of evolution and (c) fast host evolution (all other parameters are chosen according to Table 1). Trajectories are coloured light blue if they end up at the mutualistic attractor (M) and red if they end up at the antagonist one (A), thereby visualising the basins of attraction. Example trajectories highlight the three types of evolutionary transitions of interaction type described in the main text.

If host and partner evolve at comparable speeds ($v_H/v_P = 1$, Fig. 3b), stable mutualism can evolve even with an initially non-discriminating host. This can happen in two ways. First, if the partner starts as a sufficiently strong mutualist, evolution of the host's discrimination ability is fast enough to prevent evolution of antagonism in the partner. Secondly, surprisingly, if the partner initially is very antagonistic, strong positive selection lets discrimination ability of the host increase so much that the partner is finally driven towards mutualism (see dotted trajectory). For moderate antagonistic or slightly mutualistic initial values of β, evolution still ends

up at the antagonistic fixed point (potential for transitions from mutualism to antagonism and back-and-forth transitions).

Finally, if the host evolves much faster than the partner ($v_H/v_P = 10$, Fig. 3c), the basin of attraction of the antagonist attractor expands and covers large parts of the antagonist quadrant, almost ruling out transitions from antagonism to mutualism. This is the case because as soon as a partner approaches commensalism ($\beta \approx 0$), discrimination ability is selected against and its fast decrease prevents the evolution of stable mutualism.

3.3 Changing costs cause evolutionary tipping points

In order to detect evolutionary transitions between mutualism and antagonism triggered by environmental change, we vary the cost and benefit parameters in our model. Figure 4a shows the trait space with evolutionary null-isoclines for different levels of costs of mutualism c_β. Higher cost of mutualism flattens the partner null-isocline and pushes it towards antagonism. This reflects that selection on cooperativeness is dominated more and more by its costs instead of its benefits mediated by discrimination. For the evolutionary fixed points (the intersection of the evolutionary null-isoclines), this implies that for increasing c_β the two fixed points in the mutualistic region approach each other until they culminate in a unique fixed point at around $c_\beta \approx 0.3$, vanishing for higher values of c_β and leaving only the antagonistic fixed point.

The described collision of fixed points can be visualised in a bifurcation diagram showing the trait space coordinates of the fixed points depending on the parameter c_β (Fig. 4c). The change in system behaviour we observe at $c_\beta \approx 0.3$ is a saddle-node bifurcation [54] and may represent an evolutionary tipping point [55]: With increasing cost of mutualism, an interaction which resides at the stable mutualistic attractor is suddenly disrupted and evolves towards the antagonistic fixed point. Crucially, a subsequent reduction of cost cannot reverse the process.

Note that the same evolutionary tipping point is caused by a gradual reduction of the basic benefit b that the partner gets from the interaction. This is due to the fact that increasing c_β and reducing b have the same effect on the sign of the selection gradient which can be seen from

equations 2 (see Supplementary Material S.1). Also note that another evolutionary tipping point arises when costs of discrimination ability c_α increase (Fig. 4b). In this case, the host null-isocline is pushed towards lower discrimination ability α and larger absolute values of cooperativeness β. Eventually, the stable and unstable mutualistic fixed point collide and dissolve at $c_\alpha \approx 0.25$ (Fig. 4d).

Interestingly, we find that no change of parameter values leads to a gradual transition of a stable fixed point from antagonism to mutualism or vice versa. As a centrepiece of such a transition, a stable commensalistic fixed point would be needed for some parameter combination. This cannot occur in our model since the host null-isocline never crosses the commensalistic axis. In a commensalistic interaction, discrimination ability is always selected against and if it is reduced to 0, the partner evolves towards antagonism.

3.4 Individual-based simulations confirm model predictions

In general, the individual-based simulations corroborated the qualitative results from the analytical model presented in the above sections. However, by introducing stochastic mutations, they enabled trajectories to jump from one basin of attraction to the other, providing an additional source of transitions from antagonism to mutualism or vice versa. The occurrence of such jumps was positively correlated with the effect size of mutations (see Supplementary Material S.4).

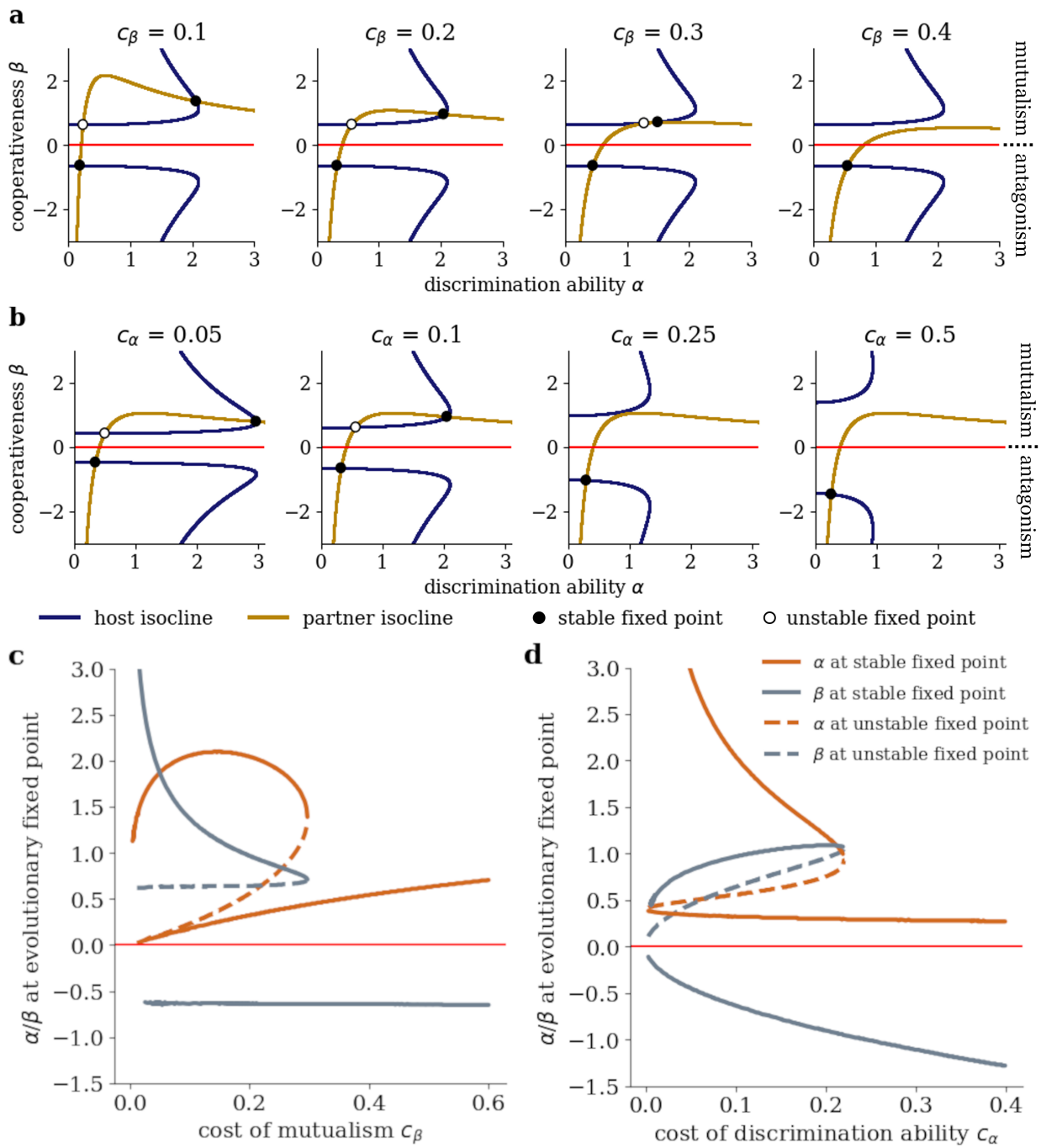

Figure 4: **Changes in interaction costs cause evolutionary tipping points.** The evolutionary null-isoclines change their shape in the trait space for varying cost of mutualism c_β (**a**) and varying cost of discrimination ability c_α (**b**). Black/white circles mark the stable/unstable evolutionary fixed points. The baseline scenario corresponds to $c_\beta = 0.2$ and $c_\alpha = 0.1$. Bifurcation diagrams show the trait values at evolutionary fixed points for varying cost of mutualistic service c_β (**c**) and cost of discrimination ability c_α (**d**). Increasing the costs eliminates the mutualistic fixed points and leaves the antagonistic fixed point as the unique attractor.

4 Discussion

The coevolution of discrimination ability of a host and cooperativeness of its partner entails gradual evolutionary transitions in the mutualism-antagonism continuum. We identified three different transition pathways under constant environmental conditions in the transient dynamics of the system when starting far from an evolutionary equilibrium state. Moreover, we detected an evolutionary tipping point: A stable mutualism is prone to an abrupt breakdown to antagonism when costs of cooperativeness or discrimination ability gradually increase in a changing environment. The robustness of these results was confirmed by stochastic individual-based simulations. In the following, we first discuss the necessary prerequisites for evolutionary transitions in the transient dynamics before outlining current theoretical developments and potential empirical tests for coevolutionary tipping points.

4.1 Determinants of transitions along the mutualism-antagonism continuum

Radical ecological change, such as a switch of the host species, colonisation of a new environment or changes in the community composition, can push biotic interactions far from an evolutionary equilibrium [5, 10]. In the transient dynamics of our model we could observe evolutionary transitions between mutualism and antagonism following such radical change. Notably, the model allowed us to investigate the role of the initial host discrimination ability for such transitions. This is particularly interesting in light of the open question whether preadaptations of host discrimination ability are a necessary prerequisite for the evolution of mutualism [56, 57].

Our results emphasise the importance of preadaptations of host discrimination ability in case of fast-evolving partners. For instance, microbial symbionts most often evolve much faster than their hosts due to smaller generation times [5]. The occurrence of transitions of interaction type then crucially relies on the initial host discrimination ability. If the interaction strength is not adapted to the level of cooperativeness of the partner in the first place, which is most likely to be the case in newly assembled interactions [58], an initially mutualistic partner will evolve towards antagonism. Only if the host already has discrimination ability, transitions from antagonism to mutualism are possible. For example, legumes probably allocated carbon to roots in response to local nitrogen availability before associating with rhizobia in the first place, thereafter selecting

for rhizobia to evolve high nitrogen fixation levels [19, 59]. However, in systems where host and partner evolve at comparable speeds, e.g. various plant-insect systems, host discrimination ability can also build up during the coevolutionary process enabling transitions to mutualism without preadapted discrimination ability.

Interestingly, after a transition from antagonism to mutualism, the interaction does not necessarily stay mutualistic. Only if the initial discrimination ability is high enough, the interaction approaches a stable mutualistic state where the partner invests in mutualism because it otherwise would be discriminated against and the host invests in discrimination ability to maintain high interaction strength with the partner. Otherwise, if the partner does not become sufficiently mutualistic, discrimination is selected against because the host is not strongly affected by the interaction. Consequently, discrimination ability of the host and thereafter also cooperativeness of the partner reduce and the interaction oscillates back to antagonism. Such back-and-forth transitions along the mutualism-antagonism continuum may be common [5, 30] but hard to detect in empirical research since transitions in both directions need to be verified and since the transient mutualism is weak.

Our results crucially depend on our notion of discrimination ability. This generalises various mechanisms such as partner choice, sanctions and partner fidelity feedback that have been proposed to enable the evolution of mutualism by reducing them to the same underlying principle: The response of the host (active or passive) depends on the service provided by the partner [33, 57]. This basic similarity is presumably the main cause for the striking lack of clear distinction of the mechanisms in the literature [19]. For instance, the selective abortion of flowers by yucca plants was given as an example for each of the three mechanisms mentioned above [22, 23, 36, 60].

However, there is a subtle difference between our model of discrimination and previous conceptions regarding the role of intraspecific variation of partner quality. In contrast to previous models of partner choice, for example, the host does not choose between different present partner individuals. Instead, it adapts the interaction strength with one present partner regardless of any alternatives. By presenting a model of evolution of discrimination ability without much

intraspecific trait variation, we provide a potential solution to the often-cited paradox that discrimination ability erases its own selective incentive by eliminating variation in partner quality [7, 20, 30].

4.2 Tipping points in the evolution of biotic interactions

In our model, a gradual change of the environmental parameters does not lead to an equally gradual transition of a stable fixed point from mutualism to antagonism or vice versa. This is because the model never exhibits stable commensalism; commensalism is always a merely transient state (in line with the scarcity of observations of persistent commensalisms in nature [61]). However, an abrupt transition from a stable mutualism to antagonism is possible when costs of cooperativeness or discrimination ability slowly increase above a certain threshold. Such a transition is characterised by a positive self-reinforcing feedback loop: Under the new environmental conditions, reduced cooperativeness of the partner selects for reduced discrimination ability of the host, which in turn selects for more antagonistic behaviour of the partner. Finally, the interaction ends up at an antagonistic equilibrium and a subsequent reduction of costs does not restore the original mutualism. Such hysteresis is inextricably linked to the occurence of tipping points [62].

Tipping point theory has proven successful in ecology by providing an explanation for abrupt regime shifts in population or community dynamics [63], and the role of evolutionary dynamics in shaping such catastrophic transitions is increasingly recognised [55, 64]. However, only few studies have identified evolutionary tipping points in the sense that a system is driven to an alternative stable state in the trait space (note that the term ”evolutionary tipping point” has also been used differently [65]). For example, plant attractiveness in a plant-pollinator interaction was shown to abruptly reduce if pollinator intrinsic growth rate falls below a threshold [66]. The application of tipping point theory to systems of multiple coevolving traits remains to the best of our knowledge unexplored. Ultimately, we believe that evolutionary tipping point theory can help to explain fundamental empirical patterns such as the observation that evolution often happens in short dynamic time intervals (or ”punctuated equilibria” [67]) followed by longer steady periods [68, 69, 70].

To date, we are not aware of any empirical attempt to detect a coevolutionary tipping point. We see two possibilities to test the predictions of our model. The first approach is based on controlled coevolution experiments with gradual variation of environmental conditions and quantification of the fitness effect of the interaction for the host in order to determine the interaction type. Some studies using the legume-rhizobium model system showed that increased nitrogen availability in the soil can lead to rapid evolution of reduced cooperativeness of rhizobia [71, 72, 73], potentially reflecting the dynamics found in our model. Here, a nitrogen-rich environment corresponds to higher costs of mutualistic service for the rhizobium since it needs to provide more nitrogen to achieve the same fitness benefit for the host plant, given that more alternative resources are available. However, no gradient of different soil treatments was used in these experiments and no test for reversibility was carried out, needed to unequivocally identify a tipping point.

Alternatively, the existence of the tipping point might also be inferred from macroevolutionary data on changes in interaction type between periods that gradually differed in interaction costs. Ideally, data sets comprise periods with environmental change in both directions to analyse reversibility of the transitions of interaction type. A major challenge in both described approaches would be to disentangle the influence of evolution (in response to environmental change) and the context-dependency of the interaction type, present without any evolution at play.

5 Conclusion

Mutualism and antagonism are increasingly recognised as spanning a continuum of possible outcomes of an interspecific interaction. We developed a theoretical framework to study how coevolution moves a two-species interaction along this continuum. We found potential for transitions from mutualism to antagonism and vice versa, depending on the initial discrimination ability of the host or in the form of evolutionary tipping points when costs gradually change. Our study thereby formulates general hypotheses for empirical work on shifts of interaction type in diverse contexts ranging from pollination to nutrient exchange symbioses. Since the interaction type has significant influence on structure and stability of complex ecological networks [74, 75], our results should have important implications for the study of communities consisting of multiple mutualistic and antagonistic interactions [11, 76, 77].

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