A unified theoretical framework for invasion in host-symbiont communities

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Statements and declarations

- The authors have no competing interests to declare that are relevant to the content of this article.
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- Data availability statement: The datasets generated or analyzed during the study are available in this published article. All the code developed for the manuscript is available on GitHub. The code is novel and original, and has been developed by author Maria M. Martignoni (2023) and can be found at `https://github.com/nanomaria/microbiallymediatedinvasion`.
- Interactive reproduction and re-parametrization of results can also be done through the modelRxiv platform (`https://modelrxiv.org/model/YfndNX`).

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Abstract

Host-symbiont communities present a unique interaction structure, in which host-symbiont interdependent fitness and the possible formation of novel host-symbiont associations can give rise to a broad range of dynamics. Understanding mechanisms that can facilitate or prevent invasion in these communities, therefore, requires to embrace a community perspective that accounts for host-host, symbiont-symbiont and host-symbiont interactions. Empirical work has shown that the formation of novel host-symbiont associations between native and invasive species can lead to multiple outcomes affecting invasion success, such as increased fitness of introduced hosts or symbionts, or decreased fitness of natives. Here, we present a unifying theoretical framework to contextualize these individual scenarios and investigate their significance at the community level, along a continuum ranging from mutualistic to parasitic host-symbiont interactions. We discuss interesting scenarios emerging from our analysis and multiple pathways through which host-symbiont interactions can facilitate or prevent host invasion, symbiont invasion, and the invasion of both hosts and their co-introduced symbionts. Our framework provides a new, mechanistic, cohesive, and intuition-enhancing tool for theoretically exploring the ways in which the subtleties of the relationships between hosts and symbionts affect invasion dynamics.

Keywords : Co-invasion, symbiont spillover, symbiont spillback, microbially mediated, microbe-mediated, linked invasion, mathematical model, differential equation, host-symbiont, mutualism, invasion, microbial invasion, plant invasion, theoretical framework, holocommunity, social microbiome

1 Introduction

Biological invasion is often regarded as invasion by a single species. However, organisms live in symbiosis with a rich and diverse collection of microbial symbionts that are an essential component of their host's fitness and reproductive success (Fitzpatrick et al., 2020; Compant et al., 2019). Microbial communities can encompass mutualistic, commensal, and parasitic (or pathogenic) symbionts that benefit or harm the host to different extents. The fitness of these symbionts, in turn, depends on their association with host partners, such that the fates of hosts and symbionts are intrinsically linked, and so are the possibilities for hosts and symbionts to successfully establish and persist in a new environment. For example, the formation of novel associations between invasive plants and pre-existing native mycorrhizal networks can facilitate the establishment of an introduced host population and its expansion into a new range (Dawkins and Esiobu, 2016; Parepa et al., 2013; Moeller et al., 2015). Novel associations between introduced symbionts and native hosts can also facilitate symbiont invasion (Díez, 2005; Wolfe and Pringle, 2012; Dickie et al., 2016), or cause the emergence of disease in native hosts (Panzavolta et al., 2021; Santini et al., 2013; Grünwald et al., 2012; Schuchert et al., 2014). In other cases, host-symbiont interactions can provide resilience to native communities. For instance, host invasiveness may be decreased by a reduction in the abundance of invasive symbionts (Zenni and Nuñez, 2013; Catford et al., 2009), or by the transmission of pathogenic agents from native to invasive hosts (Mordecai, 2013; Flory and Clay, 2013).

Awareness of the importance of host-symbiont associations in dynamics of host and symbiont invasion is growing rapidly, and so are attempts at developing conceptual frameworks to understand the impact of parasitic or mutualistic host-symbiont associations on invasion

outcomes (Dickie et al., 2017; Amsellem et al., 2017; Dunn and Hatcher, 2015; Médoc et al., 2017; Mitchell et al., 2006; Nuñez et al., 2009; Dickie et al., 2017). While some experimental evidence exists, ecological population modelling has mostly studied the range expansion and invasion dynamics of either parasite (White et al., 2018; Gubbins et al., 2000), or host populations (Lewis et al., 2016), neglecting the role of host-symbiont feedback on the invasion dynamics and often unilaterally consider how diversity and fitness of the host population can be mediated by symbiont communities (Bever et al., 1997; Yamauchi et al., 2011; Jack et al., 2017; Martignoni and Kolodny, 2023; Kandlikar et al., 2019), and not vice-versa. Host and symbiont fitness is interdependent: symbionts can influence the growth and coexistence of host populations, and changes in host populations will, in turn, influence fitness and diversity in symbiont communities, all of which can affect competitive dynamics between hosts and between symbionts. A theory of biological invasion in host-symbiont communities should therefore explicitly account for the effect that positive as well as negative host-symbiont feedback can have on both hosts and symbiont communities, and on the consequences of these effects in modulating host-host and symbiont-symbiont competition.

Theoretical insights into the stability and resilience of mutualistic and parasitic communities against invasion have been provided by network theory. These approaches have mostly focused on relating community invasiveness to network properties, such as nestedness, or connectivity (Campbell et al., 2012; Bastolla et al., 2009; Rohr et al., 2014; Vacher et al., 2010), where network structure is based on trait-based approaches considering how trait differences and similarities in the invaded and invading communities may affect interaction strength (Minoarivelo and Hui, 2016a; Hui et al., 2016; Minoarivelo and Hui, 2016b; Schleuning et al., 2015; Runghen et al., 2021). These studies may help identify common features of mutualistic or host-parasite networks, and test hypotheses regarding the relationship between structure and community-wide dynamics (Valdovinos, 2019; Bascompte and Olesen, 2015). However, particularly for the case of mutualistic networks, analyses have been performed on communities of free-living species, such as pollination or seed-dispersal mutualisms (Bascompte and Jordano, 2013), whose dynamics may differ from what is observed in host-symbiont communities. Additionally, theoretical results are largely based on Lotka-Volterra equations that may lead to inaccurate predictions due to their unrealistic biological assumptions, such as linear positive effects of mutualistic interactions and unlimited growth (Holland, 2015; Gibbs et al., 2023). Thus, the development of mathematical models that integrate biologically relevant mechanisms, such as density-dependent (instead of linear) positive effects of mutualism, while maintaining the necessary simplicity to allow analytical tractability, is key to providing a predictive understanding of the dynamics of host-symbiont communities and their potential to invade or be invaded.

We develop a mathematical framework to explore the possible invasion dynamics occurring when novel host-symbiont associations can form between native and invasive species. Our model accounts for key features of host-symbiont interactions including, critically, host-symbiont interdependent fitness and density-dependent resource exchange mechanisms, where a continuum of host-symbiont interactions ranging from mutualistic to parasitic is considered. Despite their opposite effects on host fitness, invasion dynamics driven by mutualistic or parasitic host-symbiont interactions may present similar interaction motifs (Dickie et al., 2017). For instance, the formation of mutualistic associations between invasive hosts and native mycorrhizal fungi (i.e., an association that would benefit invasive hosts) and the transmission of parasites to native hosts (i.e., an association that may weaken native hosts) may lead to similar outputs, namely providing a competitive advantage to invasive hosts and increasing their invasion success. Our model allows for the theoretical characterization of these multiple invasion pathways within a single framework, wherein a native host-symbiont community is confronted by an invasive host-symbiont community. Our framework has unifying features

that allows us to catalogue the impact and diversity of host-symbiont interactions observed experimentally and organise them in a methodological manner that can help us establish connections between similar invasion motifs and, at the same time, enhances our mechanistic understanding of biological invasion mediated by host-symbiont associations.

We will describe multiple ways by which host-symbiont interactions can facilitate or prevent host invasion, symbiont invasion, or co-invasion, defined here as the simultaneous invasion of an introduced host population and its symbiont community. We portray the model in terms that correspond best to symbioses for which microbes are primarily external to their hosts (e.g., plant-microbial symbioses), because these have been studied and described (Dickie et al., 2017; Bever et al., 2010). However, the same principles hold for systems in which the microbes are internal or partially internal to their hosts (e.g., gut or coral microbiomes, Pettay et al. (2015); Chiarello et al. (2022); Goedknegt et al. (2017)).

2 Model and Methods

2.1 Mathematical framework

To investigate the dynamics of host-symbiont communities we develop a consumer-resource model for mutualism (Holland and DeAngelis, 2010), similar to that presented by Martignoni et al. (2020). We consider a native host population with biomass p_n and its associated native symbiont community with biomass m_n. Hosts and symbiont interact by exchanging resources necessary for each other's growth. For example, in the case of the mycorrhizal symbiosis, the host plant may provide synthesized carbon in the form of sugars (e.g., glucose and sucrose) to its associated mycorrhizal fungi, and receive necessary nutrients such as phosphorus, nitrogen, or water in return (Smith and Read, 2010). The transfer of resources from hosts to symbionts increases symbiont biomass and decreases host biomass. The transfer of resources from symbionts to hosts increases host biomass and decreases symbiont biomass. We consider hosts to be facultative mutualists, and capable of some growth in the absence of the symbionts (with intrinsic growth rate quantified by the parameter r_p), while symbionts are obligate mutualists and can not grow in the absence of a host. We then extend this model to include interactions between an invasive host population (with biomass p_i) and its invasive symbiont community (with biomass m_i). We consider that native symbiont may exchange resources with native hosts, and invasive symbiont may exchange resources with native hosts. Competition between native and invasive hosts (c_p parameters) and between native and invasive symbionts (c_m parameters), may reduce their abundance, e.g., due to competition for host colonization between symbionts (Engelmoer et al., 2014; Smith et al., 2018), or due to host competition for light or other external resources (Craine and Dybzinski, 2013).

We obtain the following equations:

$$\frac{dp_n}{dt} = r_{p_n}p_n + \underbrace{q_{hp_n}\left(\boldsymbol{\alpha_{nn}} f_m^{nn} + \boldsymbol{\alpha_{in}} f_m^{in}\right)}_{\text{supply from } \mathrm{m_n} \text{ and } \mathrm{m_i}} - \underbrace{q_{cp_n}\left(\boldsymbol{\beta_{nn}} f_p^{nn} + \boldsymbol{\beta_{ni}} f_p^{ni}\right)}_{\text{supply to } \mathrm{m_n} \text{ and } \mathrm{m_i}} - \underbrace{\boldsymbol{c_{p_{in}}} p_n p_i}_{\text{competition}} - \mu_{p_n} p_n^2\,, \tag{1a}$$

$$\frac{dm_n}{dt} = \underbrace{q_{cm_n}\left(\boldsymbol{\beta_{nn}} f_p^{nn} + \boldsymbol{\beta_{in}} f_p^{in}\right)}_{\text{supply from } \mathrm{p_n} \text{ and } \mathrm{p_i}} - \underbrace{q_{hm_n}\left(\boldsymbol{\alpha_{nn}} f_m^{nn} + \boldsymbol{\alpha_{ni}} f_m^{ni}\right)}_{\text{supply to } \mathrm{p_n} \text{ and } \mathrm{p_i}} - \underbrace{\boldsymbol{c_{m_{in}}} m_n m_i}_{\text{competition}} - \mu_{m_n} m_n^2\,, \tag{1b}$$

$$\frac{dp_i}{dt} = r_{p_i}p_i + \underbrace{q_{hp_i}\left(\boldsymbol{\alpha_{ii}} f_m^{ii} + \boldsymbol{\alpha_{ni}} f_m^{ni}\right)}_{\text{supply from } \mathrm{m_i} \text{ and } \mathrm{m_n}} - \underbrace{q_{cp_i}\left(\boldsymbol{\beta_{ii}} f_p^{ii} + \boldsymbol{\beta_{in}} f_p^{in}\right)}_{\text{supply to } \mathrm{m_i} \text{ and } \mathrm{m_n}} - \underbrace{\boldsymbol{c_{p_{ni}}} p_n p_i}_{\text{competition}} - \mu_{p_i} p_i^2\,, \tag{1c}$$

$$\frac{dm_i}{dt} = \underbrace{q_{cm_i}\left(\boldsymbol{\beta_{ii}} f_p^{ii} + \boldsymbol{\beta_{ni}} f_p^{ni}\right)}_{\text{supply from } \mathrm{p_i} \text{ and } \mathrm{p_n}} - \underbrace{q_{hm_i}\left(\boldsymbol{\alpha_{ii}} f_m^{ii} + \boldsymbol{\alpha_{in}} f_m^{in}\right)}_{\text{supply to } \mathrm{m_i} \text{ and } \mathrm{m_n}} - \underbrace{\boldsymbol{c_{m_{ni}}} m_n m_i}_{\text{competition}} - \mu_{m_i} m_i^2\,. \tag{1d}$$

All of the parameters and the functions f are discussed in detail below and in SI A. A schematic representation of this model is provided in Fig. 1(a).

The transfer of resources from symbionts to hosts and from hosts to symbionts is quantified by the α_{jk} and β_{jk} parameters respectively, with subindex j representing the supplying species (n for native, or i for invasive), and subindex k representing the receiving species. These parameters may represent particular traits in the receiving and supplying species, that quantify the resource exchange capacity of each one. For instance, microbes that provide lots of phosphorus to host plants and take lots of carbon from host plants are represented by large α_j and β_j parameters. Additionally, native and invasive species can differ in their intrinsic growth rate (parameters r_{p_j}, $j = n, i$), in their efficiency at converting the resource received or supplied into biomass (parameters $q_{hp_j}, q_{cp_j}, q_{cm_j}, q_{hm_j}$, with $j = n, i$), and in the rate at which resources need to be diverted into maintenance of the existing biomass (parameters μ_{p_j} and μ_{m_j}, with $j = n, i$).

To explore the effect of host-symbiont association on invasion dynamics, we consider that parameters α_{in}, α_{ni}, β_{in} and β_{ni} can be zero or positive, depending on whether or not resource exchange between invasive symbionts/hosts and native hosts/symbionts is occurring. If invasive hosts exchange nutrients with native symbionts, parameters α_{ni} (quantifying the resource supply from native symbionts to invasive hosts) and β_{in} (quantifying the resource supply from invasive hosts to native symbionts) will assume positive values. The relationship between how much a host receives from its associated symbionts (which depends on α parameters) and how much a host gives to its associated symbionts (which depends on β parameters) per unit time determines whether a host-symbiont relationship is mutualistic or parasitic for the host or the symbiont population (see Fig. 1b). Generally, the relationship is parasitic for the host population if $\alpha \ll \beta$, and parasitic for the symbiont community if $\beta \ll \alpha$, while the interaction is mutualistic for both, hosts and symbionts, for $\alpha \simeq \beta$. A thorough explanation of the quantitative criteria used to understand whether the exchange is mutualistic or parasitic is provided below in the 'Model analysis and scenarios of interest' section.

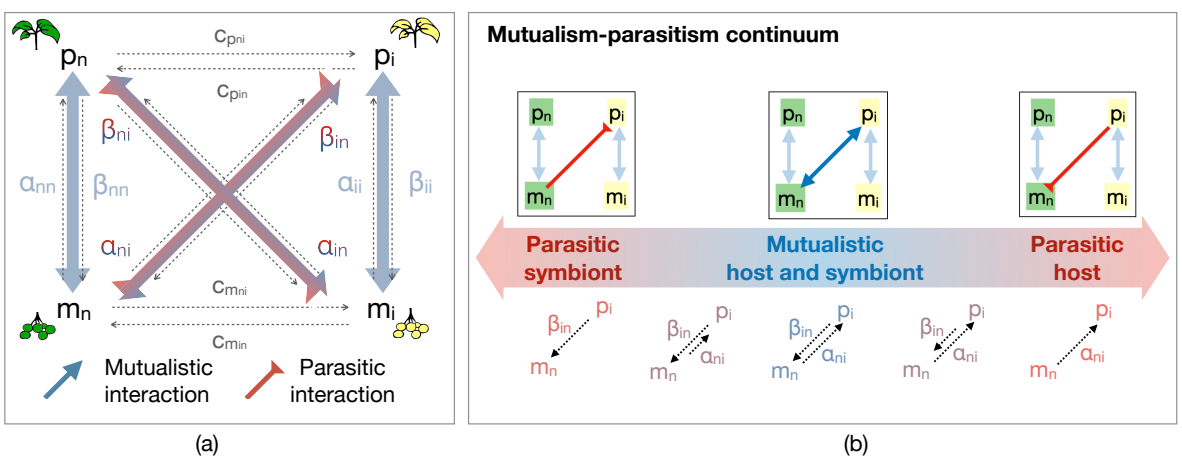

Fig. 1: Schematic representation of the model of Eq. (1). A native microbial community m_n is associated with a host population p_n. Resource exchange between hosts and symbionts is quantified by parameters α_{nn} (symbiotns to hosts) and β_{nn} (hosts to symbionts). Similarly, a population of invasive hosts p_i exchanges resources with its associated invasive symbiont community m_i (parameters α_{ii} and β_{ii}). Depending on the scenario considered, invasive hosts can also exchange resources with native symbionts, and so do invasive symbionts with native hosts (parameters α_{in}, α_{ni}, β_{in} and β_{ni}). Blue and red arrows indicate whether host-symbiont interactions are parasitic or mutualistic for hosts and symbionts, as shown in (b). Additionally, native and invasive hosts compete with each other, with competition strength quantified by parameters $c_{p_{in}}$ and $c_{p_{ni}}$, and so do native and invasive symbionts (parameters $c_{m_{in}}$ and $c_{m_{ni}}$).

In addition to resource exchange parameters, resource supply also depends on host and symbiont densities, as determined by the functions f_m and f_p. Functions f_m^{jk} are the density-dependent rates at which the microbial community m_j supplies resources to the host population p_k (or the rates at which a host population p_k receives resources from m_j), with indexes $j = n, i$ and $k = n, i$ referring to native (n) or invasive (i) populations. Functions f_p^{jk} refer to the density-dependent rates at which the host population p_j supplies resources to the microbial community m_k (or the rates at which the microbial community m_k receives resources from the host population p_j). We define:

$$f_m^{jk} = \frac{m_j p_k}{d m_j + d m_k + p_k + p_j} \quad \& \quad f_p^{jk} = \frac{p_j m_k}{p_j/d + p_k/d + m_k + m_j}\,. \tag{2}$$

The function f_p in Eq. (2) tells us that when the total host biomass is much larger than the total symbiont biomass, the amount of resource that hosts can supply is limited by symbiont biomass (i.e., by what microbes can take), adjusted by the factor $1/d$. Each host species will supply to its symbionts an amount of resource proportional to the symbiont biomass, and to the relative abundance of the host species in the whole host population. When the total host biomass is much smaller than the total symbiont biomass (adjusted by the factor $1/d$) the amount of resource that hosts can supply to their symbionts is limited by host biomass (e.g., by what the host can give). Each symbiont will supply to its host an amount of resource proportional to the host biomass, and to the proportion of biomass occupied by the symbiont in the whole symbiont community. Indeed, note that

$$f_p^{jk} \simeq \begin{cases} p_j \dfrac{m_k}{m_k + m_j} & \text{if} \quad m_k + m_j \gg (p_j + p_k)\dfrac{1}{d}, \\ m_k d \dfrac{p_j}{p_j + p_k} & \text{if} \quad m_k + m_j \ll (p_j + p_k)\dfrac{1}{d}\,. \end{cases} \tag{3}$$

Analogously, the function f_m tells us that the amount of resource that symbionts supply to hosts is limited by symbiont biomass, when the total host biomass is large compared to the total symbiont biomass, and by symbiont biomass, when the total host biomass is smaller than the total symbiont biomass (adjusted by the factor d). Indeed, note that:

$$f_m^{jk} \simeq \begin{cases} m_j \dfrac{p_k}{p_k + p_j} & \text{if} \quad p_k + p_j \gg (m_j + m_k)d, \\ \dfrac{p_k}{d} \dfrac{m_j}{m_j + m_k} & \text{if} \quad p_k + p_j \ll (m_j + m_k)d\,. \end{cases} \tag{4}$$

2.2 Model analysis and scenarios of interest

In our model, symbiont contribution to host growth and host contribution to symbiont growth vary along a continuum ranging from 'parasitic' to 'mutualistic' (see Fig. 1b). A certain host-symbiont association is defined as 'mutualistic' if the interaction increases the growth rate of both hosts and symbionts. An association is considered 'parasitic' if the biomass of either hosts or symbionts, is decreased by the interaction.

Specifically, we consider the model of Eq. 1 in the case a host population p_k is interacting with its symbiont community m_j. Variables p_k and m_j here could stand for p_n and m_n, p_i and m_i, p_n and m_i, or p_i and m_n. We obtain:

$$\begin{cases} \dfrac{dp_j}{dt} &= r_{p_j} p_j + \dfrac{p_j m_k}{\dfrac{p_j}{d} + m_k} \underbrace{\left(q_{hp_j} \dfrac{\alpha_{kj}}{d} - q_{cp_j} \beta_{jk} \right)}_{:=Q_p} - \mu_{p_j} p_j^2\,, \\ \dfrac{dm_k}{dt} &= \dfrac{p_j m_k}{\dfrac{p_j}{d} + m_k} \underbrace{\left(q_{cm_j} \beta_{jk} - q_{hm_j} \dfrac{\alpha_{kj}}{d} \right)}_{:=Q_m} - \mu_{m_k} m_k^2\,. \end{cases} \tag{5}$$

The association between p_j and m_k is mutualistic for $Q_p, Q_m > 0$, parasitic for the host population if $Q_p < 0$ and $Q_m > 0$, and parasitic for the symbiont community if $Q_p > 0$ and $Q_m < 0$ (see also SI B.2 for more details).

Note that the values of Q_p and Q_m depend on parameters α_{jk} and β_{kj}, which characterise the quality of the resource exchange between species p_j and m_k.

$$\begin{aligned} \alpha_{kj} &> \frac{q_{cp_j}}{q_{hp_j}} \beta_{jk} d \,, \\ \beta_{jk} &> \frac{q_{hm_j}}{q_{cm_j}} \frac{\alpha_{kj}}{d} \,. \end{aligned} \tag{6}$$

The two straight lines defined by Eq. (6), in α, β parameter space, mark the borders between the different regions (parasitic symbiont, mutualistic symbiont and host, and parasitic host) in Fig. 2, in which interactions between an invasive host population p_i and a native symbiont community m_n is considered (left plot), or interactions between a native host population p_n and an invasive symbiont community m_i is considered (right plot). Equality in either of Eq. (6) represents the cases in which either hosts or symbionts are commensals.

We restrict our attention to the case where the association between native hosts and native symbionts (i.e., between m_n and p_n) and between invasive hosts and invasive symbionts (i.e., between m_i and p_i) is always mutualistic. We then consider the possible outcomes when the associations between native symbionts m_n and invasive hosts p_i (Fig. 2, left) and between invasive symbionts m_i and native hosts p_n (Fig. 2, right) can be mutualistic or parasitic. We obtain seven different scenarios, which are identified in Fig. 2: (1) Invasive and native hosts do not share symbionts; a mutualistic association is observed between (2) invasive hosts and a native symbionts, or (3) native hosts and invasive symbionts; a parasitic association is observed, in which native/invasive symbionts exploit invasive/native hosts ((4) and (6)), or invasive/native hosts exploit native/invasive symbionts ((5) and (7)). The mathematical analysis of these scenarios and their biological significance will be discussed in section 3.2. Combinations of these scenarios will also be considered in section 3.3. Default parameter values used to simulate these scenarios are provided in SI A.

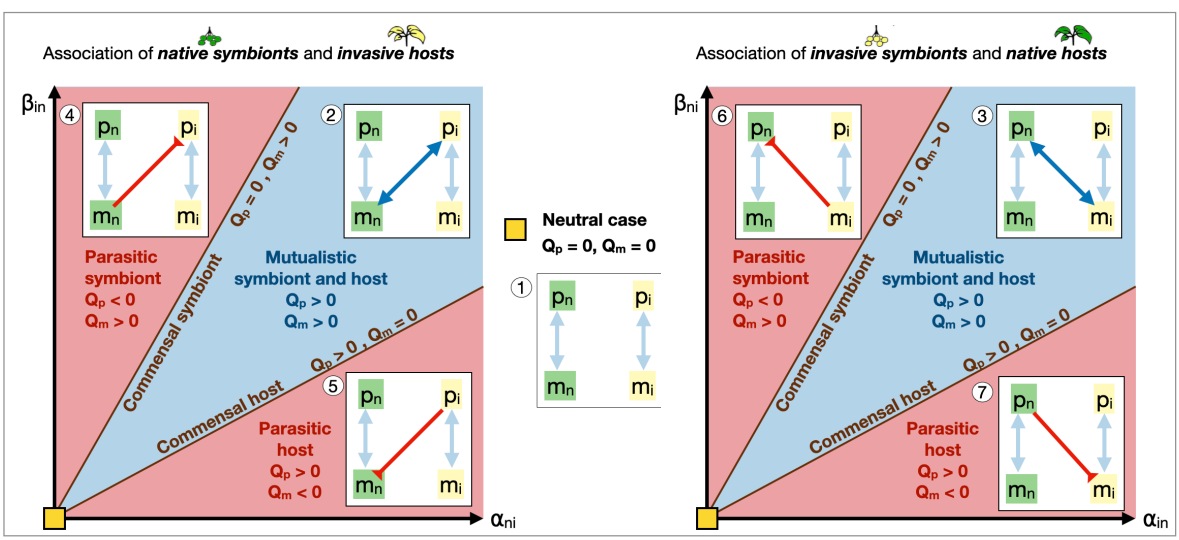

Fig. 2: Novel host-symbiont interactions can be parasitic or mutualistic, depending on the value of parameters α and β, quantifying the resource exchange capacity of hosts and symbionts (see also Fig. 1). We characterize 7 different parameter regions, corresponding to scenarios 1-7, discussed in the manuscript. Left plot: Scenarios 2, 4, and 6; Middle plot: Scenario 1; Right plot: Scenarios 3, 6, and 7. The mathematical definition of the thresholds Q_p and Q_m are provided in Eqs. (5) and (6).

3 Results

3.1 Overview of model analysis

In the following, we discuss the interesting dynamics emerging from scenarios 1-7, which shed light on the several ways in which host-symbiont interactions can lead to invasion of hosts, symbionts, or both. Note that the directionality of the interactions is important, i.e., we distinguish between the effect of hosts on symbionts, and the effect of symbionts on hosts. The outcome may be the same in separate scenarios, but the mechanism leading to these outcomes differ.

A detailed mathematical analysis of these scenarios is presented in the SI B-E, which include: the analysis of the one host - one symbiont system, which is crucial to define the parasitic/mutualistic interactions between a host population and its symbionts community (section B); the analysis of the one host - two symbiont system (section C), which is important to understand the dynamics of a host population (native or invasive) associating with both native and invasive symbionts; the analysis of the one symbiont - two hosts system (section D), providing insights on the dynamics of a symbiont community (native or invasive) associating with native and invasive hosts; and the analysis of the two hosts - two symbionts system exposed according to the scenarios described in 1-7 (section E). Exploration of alternative scenarios not presented in this paper, such as specific scenarios corresponding to different parameter combinations, can be conducted through numerical simulations of Eq. (1). For precisely this purpose, a user-friendly version of the code is made publicly available on the modelRxiv platform (Harris et al., 2022) (`https://modelrxiv.org/model/YfndNX`).

3.2 Scenarios of interest

1 Native and invasive species do not share symbionts nor hosts. When neither symbionts nor hosts are shared between native and invasive species, and competition within hosts and between symbionts is strong, competitive exclusion of one host-symbiont community, either the native or the invasive one, occurs through selection due to trait differences (represented in the model through differences in model parameters α, β, q, c, μ, or r_p), or differences in initial abundance, or through drift (not considered in this model). When selection due to trait differences occur, the host-symbiont associations that provides the highest fitness to either hosts or symbionts outcompete the other. Note that in this case, more mutualistic associations are expected to provide highest fitness, and therefore provide resilience against invasion. Differences in initial abundance can also favor one host-symbiont community over the other (see also Fig. E.1 1). Indeed, differences in the initial abundance of symbionts (or hosts) affect host (or symbiont) growth rate and, in turn, symbiont (or host) growth rate, providing a competitive advantage to the community with the largest abundance of hosts or symbionts.

2 Mutualistic association between native symbionts and invasive hosts.

- *The novel association benefits invasive hosts:* Association with native symbionts can increase the fitness of invasive hosts, and provide them with a competitive advantage that can lead to competitive exclusion of native hosts (Fig. 3b, right pathways, and SI E and Fig. E.1 2 for mathematical insights). Subsequently, invasive symbionts may outcompete native symbionts, e.g., if native symbionts are weakened by the absence of native hosts or if invasive symbionts are empowered by an increase in invasive hosts (Fig. 3a, far right pathway, leading to association between p_i and m_i). Alternatively,

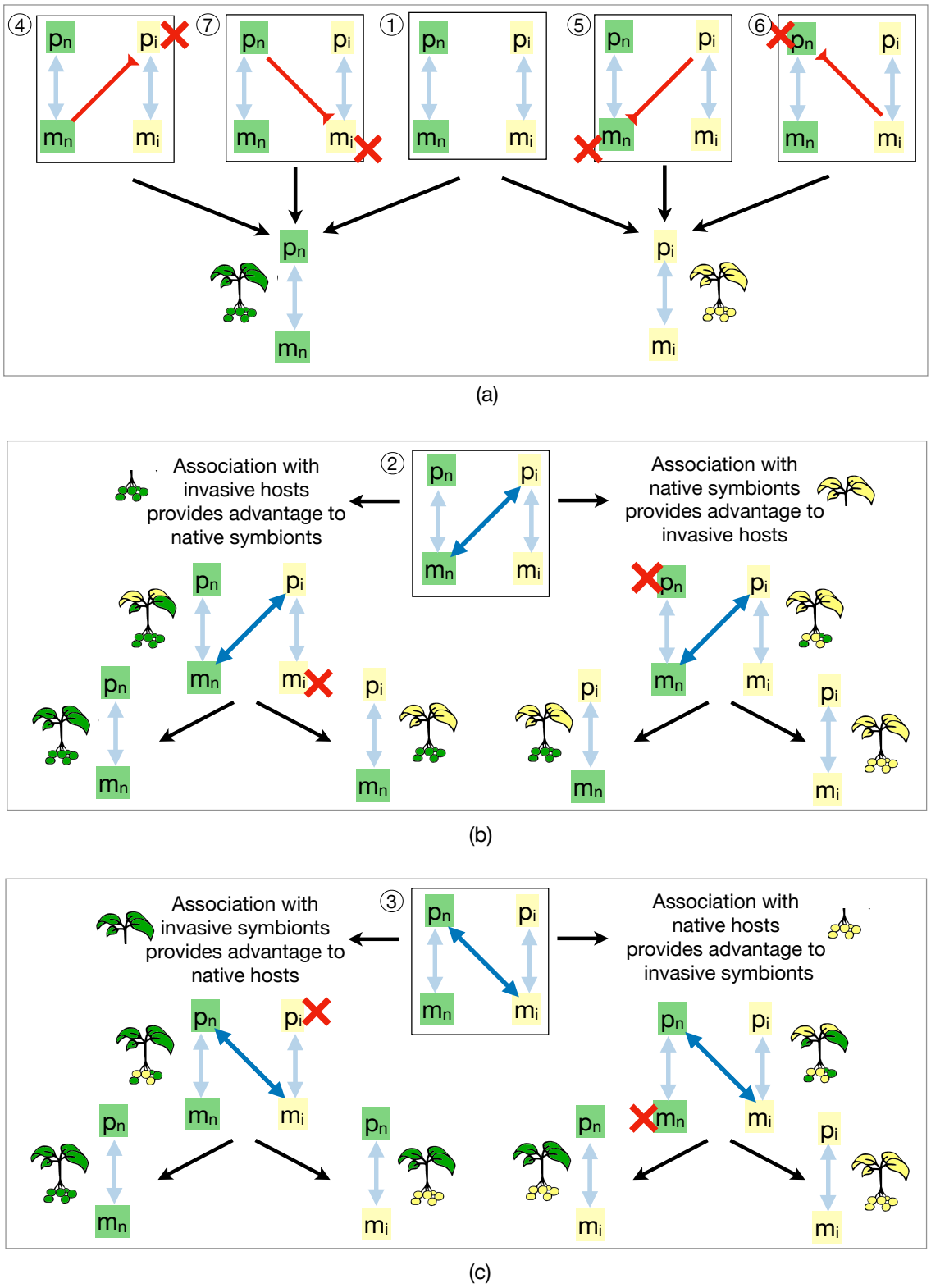

Fig. 3: Possible dynamics of invasion occurring when native species form novel host-symbiont associations with invasive species, for each of the scenarios described in Fig. 2. (a) Co-invasion can be facilitated (scenarios 5 and 6) or prevented (scenarios 4 and 7) by the formation of parasitic associations between native and invasive species. Association of (b) native symbionts with invasive hosts (scenario 2) or of (c) invasive symbionts with native hosts (scenario 3) provides a competitive advantage to hosts or symbionts, where different outcomes are observed depending on whether hosts or microbes competitively exclude each other first.

invasive symbionts may be outcompeted by native symbionts (Fig. 3a, centre right pathway, leading to association between p_i and m_n).

A variation of this scenario in which invasive hosts are low quality mutualists is discussed in (5) and in Fig. 4a. In this case, native symbionts receive a lower benefit from invasive hosts, compared to the benefit received from native hosts, but provide the same benefit to native and invasive hosts. Thus, introduced invasive hosts may grow rapidly by benefiting from the presence of a native microbial community and, indirectly, from the presence of native hosts. On the other hand, native symbionts and native hosts may suffer from the presence of invasive hosts, that benefit from native symbionts providing little in return. If this situation leads to a displacement of native hosts and symbionts, invasive hosts will no longer be able to acquire resources at little cost, and the remaining invasive host-symbiont community will have lower biomass than the initial native one.

Note that when considering the case in which native and invasive species do not share symbionts (i.e., scenario (1)) less mutualistic host-symbiont associations are expected to have lower fitness with respect to more mutualistic host-symbiont associations, and are thus not likely to invade. When accounting for the formation of novel host-symbiont associations, however, co-invasion can be driven by the exploitation of existing host-symbiont associations, where invasive hosts indirectly exploit native hosts, by receiving resources from native symbionts at low cost.

- *The novel association benefits native symbionts:* Mutualistic association with invasive hosts can also provide a competitive advantage to native symbionts, that then outcompete invasive symbionts (Fig. 3b, left pathway). No invasion occurs if invasive hosts suffer from the disruption of invasive host-symbiont associations which causes them to be outcompeted by native hosts (Fig. 3b, far left pathway, leading to association between p_n and m_n). However, if invasive symbionts are low quality mutualists to their own invasive hosts, their exclusion can provide a competitive advantage to invasive hosts, and cause the subsequent exclusion of native hosts. In this case, we observe the formation of novel associations between invasive hosts and native symbionts (Fig. 3b, center left pathway, leading to association between p_i and m_n). Note that this scenario of microbial invasion through host replacement may be more likely to occur, as it can be observed through two different pathways, namely, the centre left and right pathways in Fig. 3b (see also SI E and Fig. E.1(2) for details on the dynamics).

(3) Mutualistic association between native hosts and invasive symbionts.

- *The novel association benefits invasive symbionts:* If association with native hosts provides a competitive advantage to invasive symbionts, these may then then outcompete native symbionts (Fig. 3c, right pathways, and SI E and Fig. E.1(3) for details). The disruption of the association between native hosts and their symbionts may weaken native hosts, and lead to the establishment of invasive host-symbiont associations (Fig. 3c, far right pathway, leading to association between p_i and m_i). Alternatively, microbial invasion may be observed if invasive hosts are outcompeted by native hosts, but invasive symbionts persist in association with native hosts (Fig. 3b center right pathway, leading to association between p_n and m_i).

A variation of the latter scenario is the situation in which invasive symbionts are not completely harmful to native hosts, but are low quality mutualists. In this case, the substitution of native symbionts with invasive symbionts may lead to a loss in the biomass of native hosts (Fig. 4b). Invasive microbes may then continue to be present in the

environment and negatively affect ecosystem functionality long after the disappearance of their invasive hosts.

- *The novel association benefits native hosts:*

  Association with invasive symbionts can also provide an advantage to native hosts, which then outcompete invasive hosts (Fig. 3c, left pathway and Fig. E.1③). If invasive symbionts are strong competitors, they may subsequently exclude native symbionts, which would lead to the formation of novel associations between invasive symbionts and native hosts, and to microbial invasion (Fig. 3c center left pathway, leading to association between p_n and m_i). This scenario may be more likely to occur, as it can be observed through two different pathways. No invasion occurs if invasive symbionts suffer from the absence of invasive hosts and are outcompeted by native symbionts (Fig. 3b far left pathway, leading to associations between p_n and m_n).

④ **Native symbionts are parasitic to invasive hosts.** The association of native symbionts with invasive hosts can provide biotic resistance to native host-symbiont associations (Fig. 3a, pathway ④ and SI E and Fig. E.1④). This can occur, for example, if parasites that are only slightly harmful to native hosts, e.g., because they have co-evolved with them, cause a strong reduction in the fitness, or death, of invasive hosts. The death of invasive hosts would then be followed by the death of their symbionts. Poor adaptation of invasive species to native symbionts can also lead to exploitation of invasive hosts by native symbionts. This can occur, for example, if native symbionts weaken invasive hosts by receiving a certain resource at low cost (see also Fig. D.2 for details).

⑤ **Invasive hosts are parasitic to native symbionts.** If the invasive hosts harm microbial communities directly, e.g., by acquiring resources provided by native symbionts without giving anything in return, the interaction of invasive host and native symbionts would weaken native symbionts, and cause their displacement and the subsequent displacement of native hosts (Fig. 3a, pathway ⑤ and SI E and Fig. E.1⑤). This could be the case if the signalling dynamics between the host and the symbiont had not co-evolved. Thus, the host might be able to benefit from the symbiont against the latter's best evolutionary interest, and due to the lack of previous interactions between the organisms, the symbiont might not be able to detect and respond adaptively to the situation, creating a new type of eco-evolutionary trap scenario (Ferriere and Legendre, 2013). If invasive hosts are not completely harmful to native symbionts, but are low quality mutualists, then their association with native symbionts can lead to exploitation of pre-existing native host-symbiont associations to invade, as discussed in ② and Fig. 4(a) (see also Fig. D.2 for details).

⑥ **Invasive symbionts are parasitic to native hosts.** Co-invasion may be facilitated if invasive symbionts are harmful to native species, which would weaken native hosts and cause their competitive exclusion and the consequent exclusion of their symbionts (see Fig. 3a, pathway ⑥, and SI E and Fig. E.1⑥). This situation can occur, for example, if pathogens causing disease in native hosts are co-introduced with invasive hosts. A similar dynamics can occur if invasive symbionts are low quality mutualists, and weaken native causing their competitive exclusion by invasive hosts (see Fig. C.1).

⑦ **Native hosts are parasitic to invasive symbionts** Interaction of native hosts with invasive symbionts can provide resilience against invasion, if native hosts are harmful to invasive symbionts (Fig. 3a, pathway ⑦ and SI E and Fig. E.1⑦). Here, we consider that a

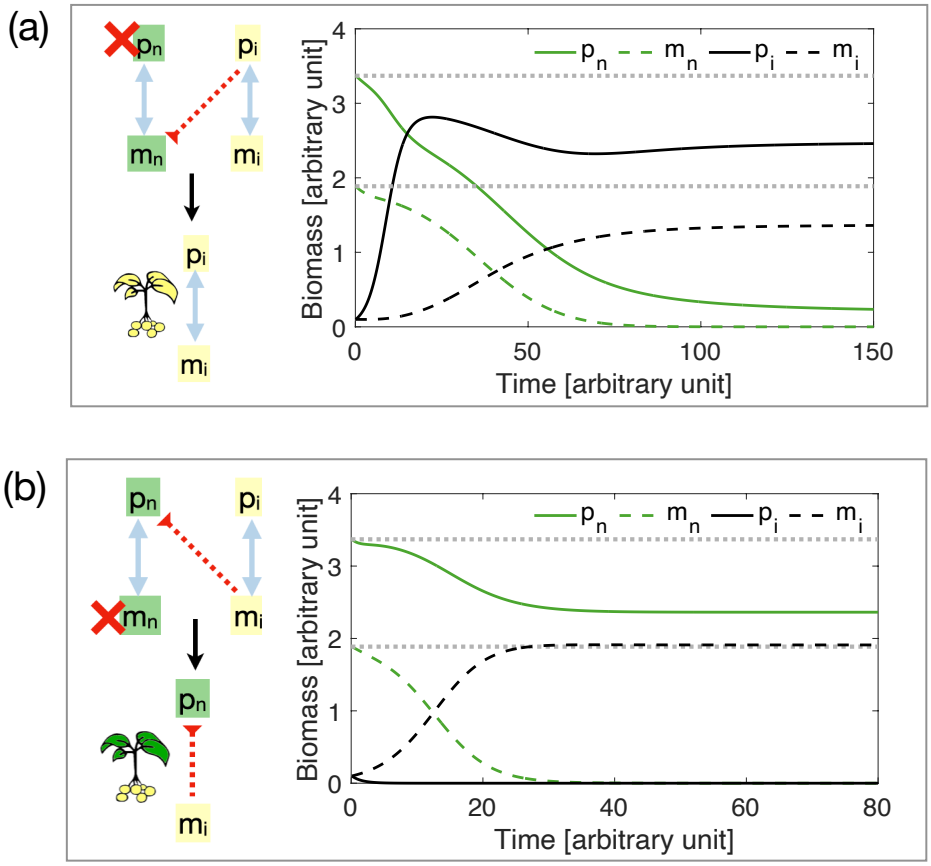

Fig. 4: (a) Possible dynamics of co-invasion occurring when invasive hosts are low quality mutualists, and exploit native symbionts at the indirect expense of native hosts. In this case, the resulting community will have lower biomass with respect to the displaced invasive community (compare black curves and dotted grey horizontal lines). (b) Possible dynamics of microbial invasion occurring when native hosts associate with invasive symbionts that are low quality mutualists. In this case, invasive symbionts persist in the environment with native hosts, where the resulting community has lower biomass than the original one. Interactive simulation of these and related scenarios can be done through the modelRxiv platform (`https://modelrxiv.org/model/YfndNX`).

native host can take advantage of invasive symbiont to the symbiont's detriment, preventing the establishment of invasive symbionts and their hosts (see also Fig. C.1).

3.3 Combined scenarios

In the previous section, we discussed the possible effect of novel host-symbiont associations on invasion dynamics. Although these scenarios were considered in isolation, and we separately explored the effect of native species on invasive ones, and of invasive species on native ones, it is also possible that both native and invasive species form novel associations at the same time (see Fig. 5). For example, the acquisition of mutualistic native symbionts by invasive hosts (strengthening invasive hosts), and the transmission of parasitic symbionts from invasive to native hosts (weakening native hosts) can both occur (see Fig. 5, third row and third column, counting from the top left), leading to the combined effect of increasing the competitive ability of invasive hosts and decreasing the competitive ability of native hosts, facilitating host invasion. Similarly, a dynamic of microbial invasion is more likely to be observed if invasive symbionts are strengthened through the formation of novel association with native

hosts, while native symbionts are harmed by invasive hosts (Fig. 5, second row, fourth column, counting from the top left).

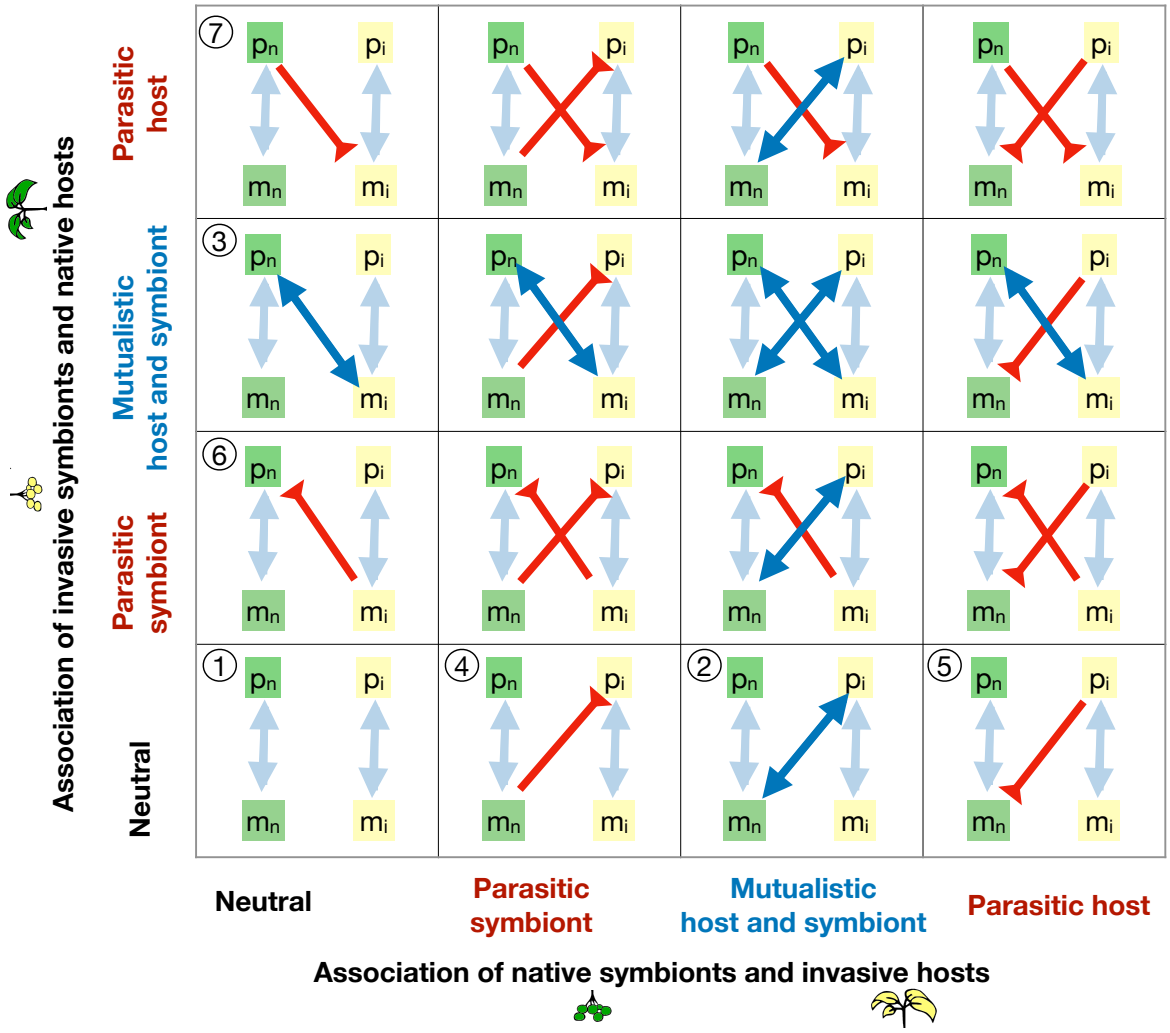

Fig. 5: Schematic representation of possible interaction scenarios that can be explored within our framework. The seven numbered circles indicate the seven scenarios discussed in the results section. Other scenarios can be understood as combination of these seven. Interactive simulation of these and related scenarios, with our default parameters or user-defined values, can be done through the modelRxiv platform (`https://modelrxiv.org/model/YfndNX`).

4 Discussion

It has been known for some time that the formation of novel host-symbiont associations can facilitate invasion, as well as provide resilience to native communities (Bever et al., 2010; Dickie et al., 2017). We show here that these general observation can be dissected into several different mechanisms which we use to create a global framework for advancing our understanding of invasion in host-symbiont communities. Furthermore, our framework allows us to organise native-invasive community interactions along a continuum of parasitic to mutualistic host-symbiont interactions.

4.1 Host-symbiont interactions increase invasion risk

A growing number of empirical studies, particularly on plant-fungal associations, have shown that invasion can occur when invasive hosts form novel mutualistic associations with native symbionts, eventually increasing host competitive ability (Callaway et al., 2004; Tedersoo et al., 2007; Moeller et al., 2015; Shipunov et al., 2008). Strong evidence also shows that pathogens co-introduced with invasive hosts may weaken native host populations, which favours their competitive exclusion by invading hosts in a dynamic often referred to as 'disease-mediated invasion' (Anderson et al., 2004; Parker and Gilbert, 2004; Desprez-Loustau et al., 2007; Santini et al., 2013; Carnegie et al., 2016). We highlight the possibility that some of these mechanisms may occur not only when shared symbionts are either pathogens or mutualists, but also when the mutualistic quality of introduced symbionts differs from that of native symbionts. For instance, introduced symbionts that are slightly less mutualistic than those found in native communities might may lead to a decrease in biomass of native hosts (Bever, 2002) (e.g., see our Fig. 4b). Similarly, the acquisition of native symbionts that are slightly more mutualistic than the original invasive community can help a host to invade (see Fig. 4a). These changes in population growth and abundance may not be sufficient to directly drive a community to extinction (as for the acquisition of pathogenic microbes), but they may be enough to provide a competitive advantage to a population with respect to another and change the invasion dynamics (Levine et al., 2004).

In addition to highlighting the possible dynamics along the mutualism-parasitism continuum, we would like to emphasize the importance of considering invasion dynamics arising at the whole community level, that accounts for host-symbiont interactions, as well as host-host and symbiont-symbiont interactions. Considering only host-symbiont interactions may lead to the misconception that only the host-symbiont community that provides the highest fitness to their hosts and symbionts may co-invade and displace native communities, as observed in some instances (Dickie et al., 2010; Nunez and Dickie, 2014; Hayward et al., 2015). However, when accounting for the possibility that symbiont disruption and exchange among native and invasive species may occur (Dickie et al., 2017; Catford et al., 2009; Mitchell et al., 2006), co-invasion of a less fit host-symbiont community may be observed (Fig. 4a). Thus, understanding the whole range of possible outcomes following the introduction of a new species in host-symbiont communities requires to embrace a community perspective that accounts for interactions among multiple hosts and symbionts (Dickie et al., 2017; Fahey and Flory, 2022).

4.2 Host-symbiont interactions increase community resilience

Less studied than the role of host-symbiont associations in invasion dynamics is their role in providing resilience to native communities (Van der Putten et al., 2010; Zenni and Nuñez, 2013; Levine et al., 2004). In spite of its importance to community assembly (Wu et al., 2024), invasion failure remains poorly understood in practice Diez et al. (2009); Zenni and Nuñez (2013). Given that novel host-symbiont associations may be key to understanding invasion success, they may also underlie the mechanisms providing resistance to invasion. Indeed, mechanisms of symbiont disruption and replacement, as well as differences in community composition and emerging properties following species introduction, may lead to changes in resource exchange dynamics between hosts and symbionts and, possibly, provide resistance to invasion (Levine et al., 2004; Dinoor and Eshed, 1984; Beckstead and Parker, 2003; Knevel et al., 2004).

A clear example of host-symbiont associations driving invasion failure is the transmission of native pathogens to invasive plants (Hood et al., 2008; Piou et al., 2002). This novel association can provide biotic resistance against invaders (Mordecai, 2013; Flory and Clay,

2013; Prevéy and Seastedt, 2015). Other, more complex, dynamics of biotic resistance occur when native symbionts, which have co-evolved with native hosts, are highly mutualistic to native hosts but not to invasive hosts (Bunn et al., 2015; Moora et al., 2011). Association with these low-quality mutualistic symbionts can harm invasive hosts, and allow for their competitive exclusion by native hosts (as described in 2 and 4).

Finally, less competitive host-symbiont pairs may resist invasion by associating with mutualistic invasive symbionts (Mordecai, 2013; Flory and Clay, 2013). Reports of spread of invasive symbionts in native habitats are numerous (Dickie et al., 2016; Wolfe and Pringle, 2012; Berch et al., 2017; Mallon et al., 2015; Hart et al., 2017; Golan et al., 2024). It is unclear, however, under which circumstances these associations can provide natives with biotic resistance to host invasion, and when they may instead lead to a risk of facilitating symbiont invasion.

4.3 Framework limitations and possible extensions

Our framework allows for the mechanistic exploration of the interactions between microbes and their hosts, and can produce a rich variety of theoretical scenarios. The feasibility of each scenario in practise, needs to be evaluated on a case-by-case basis, whereby the specificity of host-symbiont interactions and variability in their contribution to host fitness are crucial to understanding which scenarios are more likely to occur in particular settings. Parameterization based on realistic biological scenarios may provide insights into possible outcomes through numerical simulations (e.g., through the tool we provide on the modelRxiv platform Harris et al. (2022)). To narrow the gap between theory and experimental results, the framework may also be extended to account for associations between multiple hosts and symbionts (as the extension presented in SI F) to consider, for example, a microbial community composed of multiple microbial strains in which invasive hosts preferentially support certain microbial strains over others (Callaway et al., 2001; Bever, 2002; Kohout et al., 2011). Other possible extensions may consider the evolution of host-symbiont associations, such as the evolution of host adaptation to pathogens (Thrall et al., 2002), or mechanisms of 'parasite-spillback' mechanisms (Flory and Clay, 2013; Strauss et al., 2012; Kelly et al., 2009; Mangla et al., 2008; Day et al., 2016), where invasive hosts associate with native pathogens that increase in abundance on invasive hosts, leading to increased colonization of native hosts.

The framework presented here also provides a strong basis for new theoretical investigation. Our model accounts for multiple levels of interactions -such as interactions between hosts, between symbionts, and between hosts and symbiont-, it considers asymmetries in the reward that host and symbionts provide to each other, as well as an asymmetry in their dependence on the mutualism (i.e., obligate or facultative). Additionally, in our model host-symbiont interactions are characterised by biologically plausible density-dependent functional responses. Thus, the effect of higher-order interactions in our system may differ from what observed in previous studies that considered only microbial or only host communities, and that used linear, instead of density-dependent, functional responses (e.g., Gibbs et al. (2022)). An extension of our model that accounts for multiple host and symbiont populations (as in the model presented in SI F), could help us investigate the effect of higher-order interactions on coexistence and diversity of large host-symbiont communities.

5 Conclusion

Host-symbiont communities present unique characteristics that are not captured by classic frameworks. These characteristics include host-symbiont interdependent fitness, and the pos-

sible formation of novel host-symbiont associations. We present a mechanistic mathematical framework that explicitly accounts for this complexity, to advance our understanding of invasion in host-symbiont communities and to guide empirical research.

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A Numerical simulations

A.1 Overview of interaction scenarios and default parameter values

A brief description of model parameters and their default values used for the simulations is provided in Table A.1. The value of the resource exchange parameters α and β for each of the 7 scenarios described in Fig. 2 are provided in Table A.2. Specific parameters used for the plots in Fig. 4 are provided in Table A.3.

Symbol	Description	Default value
p_n	Biomass of native host population	–
m_n	Biomass of native microbial community	–
p_i	Biomass of invasive host population	–
m_i	Biomass of invasive microbial community	–
α_{jw}	Rate of microbes to hosts resource supply (j to w)	0.4 (0, 0.3)
β_{jw}	Rate of hosts to microbes resource supply (j to w)	0.4 (0, 0.3)
q_{hp_j}	Conversion factor: resources received from microbes into host biomass	5
q_{cp_j}	Conversion factor: resources supplied to microbes into host biomass	1
q_{cm_j}	Conversion factor: resources received from hosts into microbial biomass	1
q_{hm_j}	Conversion factor: resources supplied to hosts into microbial biomass	1
μ_{p_j}	Maintenance rate (hosts)	0.1
μ_{m_j}	Maintenance rate (microbes)	0.1
r_{p_j}	Intrinsic growth rate (hosts)	0.02
$c_{p_{jw}}$	Competitive effect of host population j on host population w	0.02 (weak) or 0.12 (strong)
$c_{m_{jw}}$	Competitive effect of microbial community j on microbial community w	0.02 (weak) or 0.12 (strong)
d	Default ratio of host to microbial biomass	2

Table A.1: Brief description of model's variables and parameters and their default values used for the simulations. Index $j = n, i$ and $w = n, i$ refer to native (n) or invasive (i). Values in bracket corresponds to other parameter combinations chosen for the implementation of the scenarios of Fig. 4, as provided in Table A.3. Representative parameters for the interaction scenarios presented in Fig. 2 are provided in Table A.2.

Interaction Scenario	Parameter values	
1.	$\alpha_{in} = 0$, $\beta_{ni} = 0$	; $\alpha_{ni} = 0$, $\beta_{in} = 0$
2.	$\alpha_{in} = 0$, $\beta_{ni} = 0$	; $\alpha_{ni} = \alpha$, $\beta_{in} = \beta$
3.	$\alpha_{in} = \alpha$, $\beta_{ni} = \beta$	; $\alpha_{ni} = 0$, $\beta_{in} = 0$
4.	$\alpha_{in} = 0$, $\beta_{ni} = 0$	; $\alpha_{ni} = 0$, $\beta_{in} = \beta$
5.	$\alpha_{in} = 0$, $\beta_{ni} = 0$	; $\alpha_{ni} = \alpha$, $\beta_{in} = 0$
6.	$\alpha_{in} = 0$, $\beta_{ni} = \beta$	; $\alpha_{ni} = 0$, $\beta_{in} = 0$
7.	$\alpha_{in} = \alpha$, $\beta_{ni} = 0$	; $\alpha_{ni} = 0$, $\beta_{in} = 0$

Table A.2: Possible parameter values of resource exchange rates between native microbes and invasive hosts (α_{ni} and β_{in}) and between native hosts and invasive microbes (α_{in} and β_{ni}), for the given interaction scenarios of Fig. 2.

Figure	Parameter	Value	Figure	Parameter	Value
4a	α_{ii}	0.3	4b	α_{ii}	0.3
	β_{ii}	0.3		β_{ii}	0.3
	α_{ni}	0.4		α_{ni}	0
	β_{in}	0.3		β_{in}	0
	α_{in}	0		α_{in}	0.3
	β_{ni}	0		β_{ni}	0.4
	$c_{m_{in}}$	0.12		$c_{m_{in}}$	0.12
	$c_{m_{ni}}$	0.02		$c_{m_{ni}}$	0.02
	$c_{p_{in}}$	0.02		$c_{p_{in}}$	0.12
	$c_{p_{ni}}$	0.02		$c_{p_{ni}}$	0.12

Table A.3: Brief description of model parameters used to produce Fig. 4. Other parameter values corresponds to those listed in Table A.1.

A.2 Scenarios on ModelRxiv

Scenarios of interest are uploaded on the modelRxiv platform, at the following link: `https://modelrxiv.org/model/YfndNX`. The website allows the reproduction and re-parametrization of the 7 interaction scenarios of Fig. 2, as shown in Fig. A.1, and the interactive reproduction of Fig. 4.

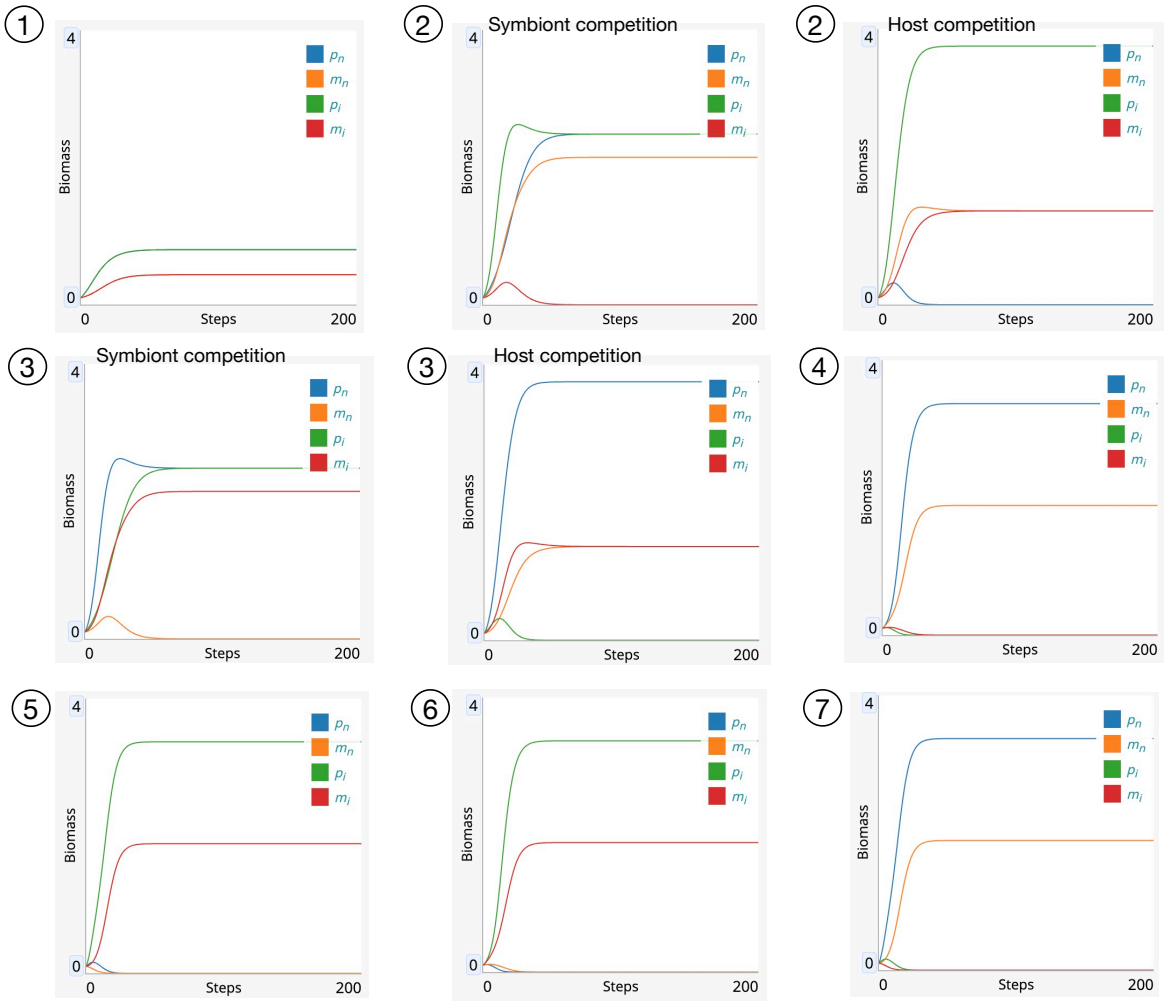


Fig. A.1: Timeseries produced by scenarios 1-7 described in Fig. 2, for the parameter combinations provided in Table A.2 and Table A.2. Note that in scenarios 2 and 3 coexistence of hosts or symbionts is unstable when competition is strong, and differences in model parameters or in initial conditions will lead to competitive exclusion of one of the two hosts and one of the two symbionts. The same steady states are stable only for weak competition, as discussed in SI E.1.4.

B Analysis of the one host and one symbiont case

We here consider the association of one host, with biomass p and intrinsic growth rate r_p, that transfers resources to a symbiont at rate β. The symbiont, with biomass m, transfers resources to the host at a rate α. The dynamics of their interaction is described by the model of Eq. (5):

$$\begin{cases} \dfrac{dp}{dt} &= r_p p + \dfrac{pm}{\dfrac{p}{d}+m} Q_p(\alpha,\beta) - \mu_p p^2\,, \\ \dfrac{dm}{dt} &= \dfrac{pm}{\dfrac{p}{d}+m} Q_m(\alpha,\beta) - \mu_m m^2\,, \end{cases} \quad \text{where} \quad \begin{cases} Q_p(\alpha,\beta) &= q_{hp}\dfrac{\alpha}{d} - q_{cp}\beta\,, \\ Q_m(\alpha,\beta) &= q_{cm}\beta - q_{hm}\dfrac{\alpha}{d}\,. \end{cases} \tag{7}$$

The quantities Q_p and Q_m represent respectively the net gain of the plant and the net gain of the symbiont.

B.1 Steady state existence

The system of Eq. (7) presents three steady states: The extinction steady state $(0,0)$, the symbiont-free steady state $(p_0,0)$ with $p_0 = r_p/\mu_p > 0$, and the coexistence steady state (p^*,m^*), which is observed as long as $Q_p + r_p > 0$ and $Q_m > 0$. The positive coexistence steady state (p^*,m^*) is given by

$$p^* = p_0 + \frac{\dfrac{Q_p Q_m}{\mu_m \mu_p}}{\dfrac{S_1}{d} + \dfrac{Q_m}{\mu_m}}\,, \text{ and } m^* = \frac{d\,Q_m}{\mu_m}\frac{\dfrac{S_1}{d}}{\dfrac{S_1}{d}+\dfrac{Q_m}{\mu_m}} \tag{8}$$

where

$$S_1 = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d}\right)^2 + p_0\frac{Q_m}{\mu_m} + \frac{Q_m\,Q_p}{\mu_m\,\mu_p}}\,.$$

The phase plane of the system of Eq. 7, with corresponding steady states and nullclines is shown in Fig. B.1.

B.2 Parasitic/mutualistic hosts and symbionts

The description of the parasitic/mutualistic interaction are summarized in Fig. 2 and explained in detail in Fig. B.2.

Mutualistic/parasitic symbiont. When $Q_p > 0$, that is for

$$\alpha \geq q_{cp}/q_{hp}\beta\,d,$$

the growth rate of the host in association with the symbiont is always larger than the biomass of the host alone (p_0). In this case the symbiont is *mutualistic* to the host.

Conversely, when $Q_p < 0$, that is $0 < \alpha \leq q_{cp}/q_{hp}\beta\,d$, the growth rate of the host is reduced compared to its growth rate alone. In this case we say that the symbiont is *parasitic*. If the symbiont is highly parasitic, or if the intrinsic growth rate of the host in the absence of the symbiont is low, the parasitic symbiont can drive the host to extinction. This occurs for

$$\left(\frac{p_0}{2d}\right)^2 + p_0\frac{Q_m}{\mu_m} + \frac{Q_m\,Q_p}{\mu_m\,\mu_p} < 0.$$

In this case, we say that the symbiont is *pathogenic*.

Mutualistic/parasitic host. Similarly, if $Q_m > 0$, that is β is large enough, such that

$$\beta \geq q_{hm}/q_{cm}\alpha/d,$$

the biomass of the symbiont is positive and the host is *mutualistic* to the symbiont. While if $Q_m \leq 0$, that is $\beta \leq q_{hm}/q_{cm}\alpha/d$, the positive steady state does not exists and the host is *parasitic* to the symbiont. In this case, the host drives the symbiont toward extinction, as symbionts in this model are obligate mutualists.

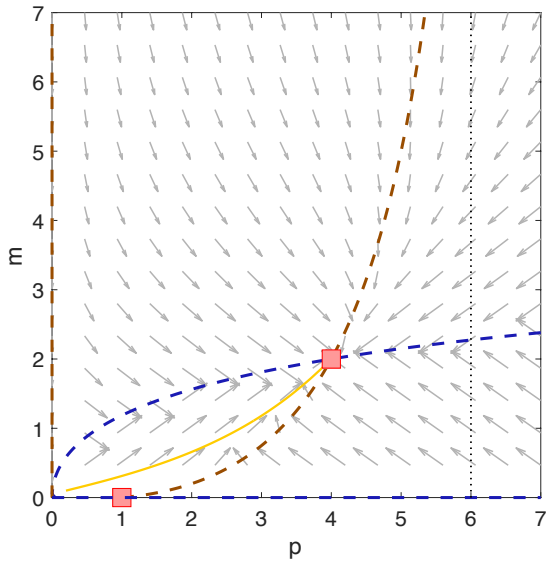


Fig. B.1: (a) Phase plane corresponding to the system of equations (7), for which $r_p > 0$. Brown dashed lines are nullclines found for $dp/dt = 0$, while blue dashed lines are nullclines found for $dm/dt = 0$. Intersection of the two non-zero nullclines corresponds to the stable steady state (p^*, m^*), represented by the red square. Intersection of the $dp/dt = 0$ nullcline with the horizontal axis corresponds to the steady state $(p_0, 0)$, in which the host reaches a symbiont-free steady state. The vertical black dotted line corresponds to the asymptote $p = Q_p/\mu_p$.

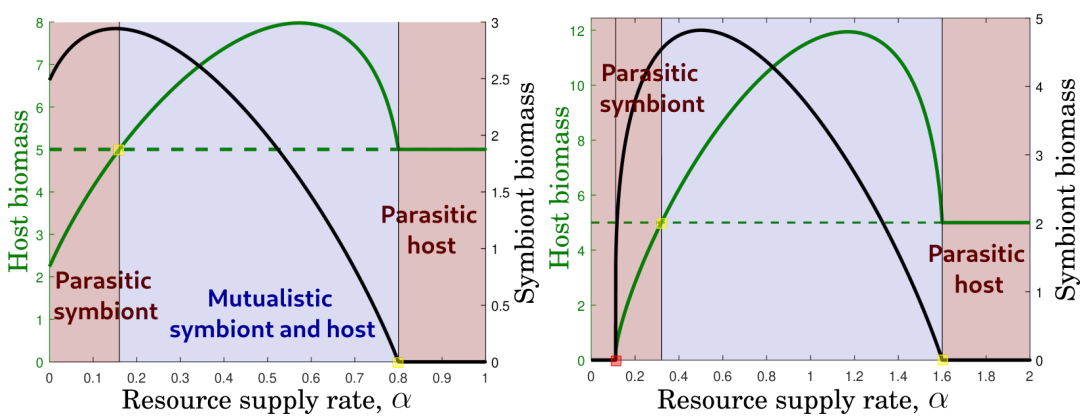


Fig. B.2: Host (green plain curve) and symbiont (black plain curve) biomass at equilibrium (p^*, m^*) defined by (8), with respect to the resource exchange rate α of the symbiont. The host exchange rate β is fixed to $\beta = 0.4$ (left panel) and $\beta = 0.8$ (right panel). The dashed line corresponds to the biomass of the host alone $p_0 = r_p/\mu_p$, with $r_p = 0.5$. The yellow squares correspond to the critical values when symbiont becomes parasitic, i.e., when $\alpha = q_{cp}/q_{hp}\beta\, d$ (left square), and when host becomes parasitic (right square), i.e., when $\alpha = \beta d q_{cm}/q_{hm}$ The red square corresponds to the threshold when parasitic symbiont become pathogenic, meaning that the host can not grow in the presence of the symbiont.

B.3 Steady state stability

To derive the stability of the steady state (p^*, m^*), we compute the Jacobian of the system of equation (7). We obtain:

$$J(p^*, m^*) = \frac{1}{\frac{p^*}{d} + m^*} \begin{pmatrix} \frac{m^{*2}}{\frac{p^*}{d} + m^*} Q_p + (r_p - 2\mu_p p^*)\left(\frac{p^*}{d} + m^*\right) & \frac{\frac{p^{*2}}{d}}{\left(\frac{p^*}{d} + m^*\right)} Q_p \\ \frac{m^{*2}}{\left(\frac{p^*}{d} + m^*\right)} Q_m & \frac{\frac{p^{*2}}{d}}{\frac{p^*}{d} + m^*} Q_m - 2\mu_m m^* \left(\frac{p^*}{d} + m^*\right) \end{pmatrix}. \tag{9}$$

From Eq. (7), we know that at steady state

$$\begin{cases} \frac{m^*}{\frac{p^*}{d} + m^*} Q_p = \mu_p p^* - r_p = \mu_p (p^* - p_0) \\ \frac{p^*}{\frac{p^*}{d} + m^*} Q_m = \mu_m m^* \,. \end{cases}$$

Thus the Jacobian J can be written as

$$J(p^*, m^*) = \frac{1}{\frac{p^*}{d} + m^*} \begin{pmatrix} -\mu_p p^* \left(m^* + \frac{2p^* - p_0}{d}\right) & \mu_m m^* \frac{p^*}{d} \frac{Q_p}{Q_m} \\ \mu_p m^* \frac{Q_m}{Q_p} \left(p^* - p_0\right) & -\mu_m m^* \left(2m^* + \frac{p^*}{d}\right) \end{pmatrix}.$$

First, we have $\mathrm{Tr}(J) < 0$. If $Q_p \geq 0$, then $p^* > p_0$ and the inequality follows. Conversely, if $Q_p < 0$ we have

$$\begin{aligned} \mathrm{Tr}(J) &= -\mu_p p^* \left(m^* + \frac{2p^* - p_0}{d}\right) - \mu_m m^* \left(2m^* + \frac{p^*}{d}\right) \\ &= -(\mu_p p^* + \mu_m m^*) \left(m^* + \frac{p^*}{d}\right) - \mu_p p^* \frac{p^* - p_0}{d} - \mu_m m^{*2} \\ &= -(\mu_p p^* + \mu_m m^*) \left(m^* + \frac{p^*}{d}\right) - \frac{p^*}{d} \frac{m^*}{\frac{p^*}{d} + m^*} Q_p - m^* \frac{p^*}{\frac{p^*}{d} + m^*} Q_m < 0 \,. \end{aligned}$$

The inequality holds true if $Q_m > -Q_p/d$, that is equivalent to $q_{cm} > q_{cp}/d$ and $q_{hm} < q_{hp}/d$, which imposes that

$$\frac{q_{hp} q_{cm}}{q_{cp} q_{hm}} > 1.$$

To prove stability of (p^*, m^*) we should therefore show that $\mathrm{Det} J > 0$. We have

$$\begin{aligned} \mathrm{Det} J &= \mu_m \mu_p m^* p^* \left(m^* + \frac{2p^* - p_0}{d}\right) \left(2m^* + \frac{p^*}{d}\right) - \mu_p \mu_m m^{*2} \frac{p^*}{d} (p^* - p_0) \\ &= \mu_m \mu_p m^* p^* \left(m^* + \frac{p^*}{d}\right) \left(2\left(m^* + \frac{p^*}{d}\right) - \frac{p_0}{d}\right) > 0 \,. \end{aligned}$$

The positivity of the determinant follows from the following inequality

$$\begin{aligned} 2\left(m^* + \frac{p^*}{d}\right) - \frac{p_0}{d} &= 2S_0 - \frac{p_0}{d} \\ &= \sqrt{\left(\frac{p_0}{2d}\right)^2 + \frac{Q_m}{\mu_m} p_0 + \frac{Q_m Q_p}{\mu_m \mu_p}} > 0 \,. \end{aligned}$$

Therefore, we showed that when the unique positive stable steady state (p^*, m^*) exists, that is when $r_p \geq 0$, $Q_m > 0$ and $\left(\frac{p_0}{2d}\right)^2 + p_0 \frac{Q_m}{\mu_m} + \frac{Q_m\, Q_p}{\mu_m\, \mu_p} \geq 0$, then it is stable. The temporal dynamics of p and m over time is shown in Fig. B.1b.

However, when $Q_m < 0$, then the free-symbiont steady state $(p_0, 0)$ becomes stable because its jacobian is

$$J(p_0, 0) = \begin{pmatrix} -r_p & d\, Q_p \\ 0 & d\, Q_m \end{pmatrix}.$$

C Analysis of the one host and two symbionts case

We consider the case in which one native host p_n is associated with 2 symbionts (the native symbiont m_n and the invasive symbiont m_i) which compete between each other with competition strength c. The corresponding differential equation system, is given by:

$$\begin{cases} \dfrac{dp_n}{dt} &= r_p\, p_n + \dfrac{p_n}{\dfrac{p_n}{d} + m_n + m_i} \left(Q_{p_n} m_n + Q_{p_i} m_i\right) - \mu_p p_n^2\,, \\ \dfrac{dm_n}{dt} &= \dfrac{Q_{m_n} p_n m_n}{\dfrac{p_n}{d} + m_n + m_i} - \mu_m m_n^2 - c m_n\, m_i\,, \\ \dfrac{dm_i}{dt} &= \dfrac{Q_{m_i} p_n m_i}{\dfrac{p_n}{d} + m_n + m_i} - \mu_m m_i^2 - c m_n\, m_i\,. \end{cases}$$

The host is either obligate or facultative mutualists ($r_p \geq 0$). The native host and the native symbionts are mutualistic, while the native host and the invasive symbiont might be either parasitic or mutualistic. In particular their exchange rates are given by

$$\begin{cases} Q_{p_n} = q_{hp} \dfrac{\alpha_{nn}}{d} - q_{cp} \beta_{nn} > 0 \\ Q_{m_n} = q_{cm} \beta_{nn} - q_{hm} \dfrac{\alpha_{nn}}{d} > 0 \end{cases} \quad \text{and} \quad \begin{cases} Q_{p_i} = q_{hp} \dfrac{\alpha_{in}}{d} - q_{cp} \beta_{ni}\,, \\ Q_{m_i} = q_{cm} \beta_{ni} - q_{hm} \dfrac{\alpha_{in}}{d}\,. \end{cases}$$

C.1 Steady state existence

To compute the steady state, we define the two following vectors $\mathbf{Q}_p$, $\mathbf{Q}_m$ of net gain and the competition matrix $\mathbf{C}_m$

$$\mathbf{Q}_m = \begin{pmatrix} Q_{m_n} \\ Q_{m_i} \end{pmatrix} \quad \text{and} \quad \mathbf{Q}_p = \begin{pmatrix} Q_{p_n} & Q_{p_i} \end{pmatrix} \quad \text{and} \quad \mathbf{C}_m = \begin{pmatrix} \mu_m & c \\ c & \mu_m \end{pmatrix},$$

and the two quantities: the free-symbiont equilibrium of the host p_0 and the total biomass of the system S;

$$p_0 = \frac{r_p}{\mu_p} \quad \text{and} \quad S = \frac{p}{d} + m_n + m_i.$$

The competition matrix can be reformulate as follows $\mathbf{C}_m = (\mu_m - c)I + c\mathbf{1}$, where $\mathbf{1}$ is the matrix full of 1 and I is the identity matrix. Thus the matrix $\mathbf{C}_m$ is invertible if and only if

$$\mu_m \neq c.$$

and its inverse satisfies

$$\mathbf{C}_m^{-1} = \frac{1}{\mu_m - c} I - \frac{c}{(\mu_m - c)(\mu_m + c)} \mathbf{1}\,.$$

Coexistence steady state A positive steady state (p, m_n, m_i), that we write $(p, \mathbf{m})$ with $\mathbf{m} = (m_n, m_i)$, will satisfy the following problem

$$\frac{1}{S}\mathbf{Q}_p\mathbf{m} = \mu_p p - \mu_p p_0 \quad \text{and} \quad \frac{1}{S}\mathbf{Q}_m\, p = \mathbf{C}_m\mathbf{m}\,.$$

By combining the two systems, we obtain

$$\frac{\mathbf{C}_m^{-1}\mathbf{Q}_m\mathbf{Q}_p}{\mu_p}\mathbf{m} = S^2\mathbf{m} - S\mathbf{C}_m^{-1}\mathbf{Q}_m p_0 \quad \text{and} \quad \frac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}p = S^2\,(p - p_0)\ .$$

We can reformulate the system as follows:

$$p = \frac{S^2\, p_0}{S^2 - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}} \quad \text{and} \quad (S^2\, I - \mathbf{A})\mathbf{m} = S\mathbf{q}_0\,,$$

where $\mathbf{A} = \dfrac{\mathbf{C}_m^{-1}\mathbf{Q}_m\mathbf{Q}_p}{\mu_p}$ and $\mathbf{q}_0 = \mathbf{C}_m^{-1}\mathbf{Q}_m\, p_0$.

Observing that $\mathrm{Tr}(\mathbf{A}) = \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}$ and $\mathbf{A}^k = \left(\dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}\right)^k\mathbf{A}$ for any $k \geq 2$, we deduce that

$$\begin{aligned}
(S^2 I - \mathbf{A})^{-1} \quad & \frac{1}{S^2}\left(I - \frac{\mathbf{A}}{S^2}\right)^{-1} = \frac{1}{S^2}\sum_{k\geq 0}\left(\frac{\mathbf{A}}{S^2}\right)^k \\
& \frac{1}{S^2}\left(I + \sum_{k\geq 1}\left(\frac{1}{S^2}\frac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}\right)^k\mathbf{A}\right) \\
& = \frac{1}{S^2}\left(I + \frac{\mathbf{A}}{S^2 - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}}\right) = \frac{S^2 I + \left(\mathbf{A} - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}I\right)}{S^2\left(S^2 - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}\right)}\,.
\end{aligned}$$

We can compute $\mathbf{m}$ as follow

$$\mathbf{m} = (S^2 I - \mathbf{A})^{-1} S\,\mathbf{q}_0 = \frac{S^2\mathbf{q}_0 + \left(\mathbf{A} - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}I\right)\mathbf{q}_0}{S(S^2 - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p})} = \frac{S\mathbf{C}_m^{-1}\mathbf{Q}_m p_0}{S^2 - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}}\,.$$

Thus from the definition of S, we obtain the following equation

$$\begin{aligned}
S \quad &= \frac{p}{d} + \mathbf{e}\,\mathbf{m} \\
&= \frac{1}{d}\frac{S^2\, p_0}{S^2 - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}} + \frac{S\mathbf{e}\mathbf{C}_m^{-1}\mathbf{Q}_m p_0}{S^2 - \dfrac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}}\,,
\end{aligned}$$

where $\mathbf{e} = (1, \ldots, 1)$. We show that S is the positive root of the following second order polynomial

$$S^2 - \frac{p_0}{d}S - \left(\mathbf{e}\mathbf{C}_m^{-1}\mathbf{Q}_m p_0 + \frac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}\right)\,.$$

Finally, using the property of $\mathbf{C}_m^{-1}$, we can show that

$$\mathbf{e}\mathbf{C}_m^{-1}\mathbf{Q}_m = \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c} \quad \text{and} \quad \frac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p} = \frac{\mathbf{Q}_p\mathbf{Q}_m}{\mu_p(\mu_m - c)} - \frac{c\,(\mathbf{e}\mathbf{Q}_m)(\mathbf{e}\mathbf{Q}_p)}{(\mu_m - c)(\mu_m + c)\mu_p}\,,$$

and we deduce that S is given by

$$S = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d}\right)^2 + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c} p_0 + \frac{\mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m}{\mu_p}}\,.$$

Finally, we get

$$p = p_0 + \frac{\dfrac{\mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m}{\mu_p}}{\dfrac{S}{d} + \dfrac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c}} \quad \text{and} \quad \mathbf{m} = \frac{S}{\dfrac{S}{d} + \dfrac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c}} \mathbf{C}_m^{-1} \mathbf{Q}_m\,. \tag{10}$$

Coexistence steady exists only under weak competition. The coexistence steady state is positive if and only if S exists and the components of $\mathbf{m}$ are positive, that is when the following inequality hold true:

$$\left(\frac{p_0}{2d}\right)^2 + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c} p_0 + \frac{\mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m}{\mu_p} > 0, \quad \mu_m Q_{m_n} - c Q_{m_i} > 0 \quad \text{and} \quad \mu_m Q_{m_i} - c Q_{m_n} > 0$$

The two last inequalities imposes that

$$c < \mu_m \quad \text{and} \quad \frac{\mu_m}{c} Q_{m_n} > Q_{m_i} > \frac{c}{\mu_m} Q_{m_n} > 0.$$

Thus, the coexistence steady state does exist if the **symbionts compete weakly ($c < \mu_m$)**, the host is not *parasitic* to the invasive symbiont ($Q_{m_i} < \mu_m\, Q_m/c$) and the invader symbiont has no *competing advantage* over the native symbiont ($Q_{m_i} > c\, Q_m/\mu_m$).

C.2 Parasitic versus mutualistic behaviour of host and symbiont

We here investigate the different nature of the interactions between two symbionts (a native and an invasive one) and a host, when the host is initially associated with a native symbiont, that can competes with the invasive symbiont.

Parasitic host. A host associated with a native mutualistic symbiont can be parasitic to an invasive symbiont, that competes with the native symbiont ($Q_{m_i} < \mu_m\, Q_m/c$). The host can be parasitic to the invasive symbiont even if it would have been mutualistic to it in absence of the native symbiont ($Q_{m_i} > 0$). This detrimental effect of the host associated with a native symbiont is due to competition between the two symbionts (see rightmost yellow square in Fig. C.1(b) that shows the transition between mutualistic and parasitic host). Thus the association with a mutualistic symbiont can enhance the parasitic nature of the host with respect to invasive symbionts (compare dashed curve $Q_{m_i} = 0$ with plain curve $Q_{m_i} = \mu_m\, Q_m/c$ in Fig. C.1(a)).

Pathogenic invasive symbiont. A invasive symbiont is *pathogenic* if it drives the host to extinction. This situation occurs when the exchange rates satisfies the following conditions

$$\left(\frac{p_0}{2d}\right)^2 + \frac{Q_{m_i}}{\mu_m} p_0 + \frac{Q_{p_i} Q_{m_i}}{\mu_p} < 0$$

The transition between a pathogenic and a parasitic symbiont is illustrated by the leftmost red square in Fig. C.1.

Substitution of native symbiont with invasive symbiont. If the invasive symbiont has a competing advantage over the native symbiont, that is $Q_{m_i} < c\,Q_m/\mu_m$, then the coexistence steady state does not exist and the invasive symbiont replaces the native symbiont. In this case, the invasive symbiont has a *competing advantage over the native symbiont*. The transition between symbiont substitution and coexistence is depicted by the rightmost red square in Fig. C.1.

The invasive symbiont can be either parasitic or mutualistic to the native host depending on their exchange rates. For instance in absence of native species, the previous definition of section B.2 states that if $Q_{p_i} > 0$ the invasive symbiont is *mutualistic* to the host, while if $Q_{p_i} > 0$ then the symbiont is also *parasitic* to the host. However, this definition only compare the biomass of the host with and without the invasive symbiont. In presence of initial native symbiont, we may also compare with the host biomass when associated with the mutualistic native symbiont. We discuss the parasitic/mutualistic nature of the invasive symbiont with respect to the native host in the following paragraph.

Mutualistic/parasitic invasive symbiont. In the presence of a native symbiont, the mutualistic nature of the interaction between the native host and the invasive symbiont may vary when comparing with the scenario without a native symbiont, that competes with the invasive symbiont. In both situations, the invasive symbiont is *mutualistic* to the host, if the biomass of the native host is larger than the biomass of the native host when alone with or without its native symbiont.

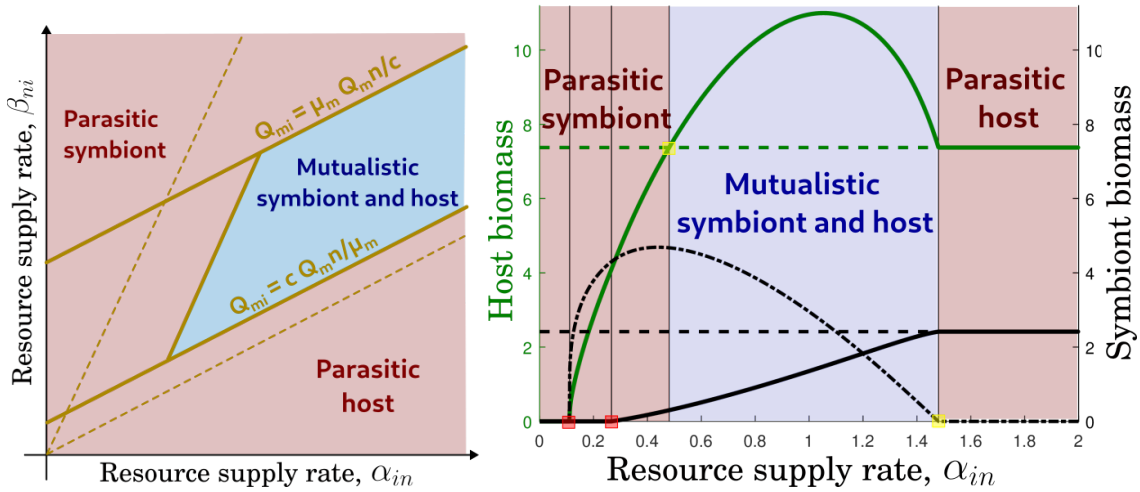
When the native and invasive symbionts persist at equilibrium, that is $Q_{m_i} > c\,Q_m/\mu_m$, the invasive symbiont is *mutualistic* when the exchange rates between the native host and the invasive symbiont are such that

$$\frac{\mu_m \mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m}{S^2} \geq \frac{Q_{p_n} Q_{m_n}}{S_n^2} \quad \text{where} \quad S_n = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d}\right)^2 + \frac{Q_{m_n}}{\mu_m} p_0 + \frac{Q_{p_n} Q_{m_n}}{\mu_p \mu_m}}\,.$$

The transition between a mutualistic and parasitic invasive symbiont is illustrated by the leftmost yellow square in Fig. C.1.

When the invasive symbiont replaces the native symbiont, that is $Q_{m_i} \leq c\,Q_m/\mu_m$, then the invasive symbiont is mutualistic if the biomass of the host is larger than the biomass of the host when associated with its initial native symbiont. This situation occurs when

$$\frac{Q_{p_i} Q_{m_i}}{S_i^2} \geq \frac{Q_{p_n} Q_{m_n}}{S_n^2} \quad \text{where} \quad S_{n/i} = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d}\right)^2 + \frac{Q_{m_{n/i}}}{\mu_m} p_0 + \frac{Q_{p_{n/i}} Q_{m_{n/i}}}{\mu_p \mu_m}}\,.$$



(a) (b)

Fig. C.1: Parasitic or mutualistic invasive symbiont and native host. Evolution of the host (green plain curve) and symbiont (black plain curve) biomass at equilibrium defined by (10), with respect to the exchange rate α_{in} of the invasive symbiont to the native host. The exchange rates between native pair are fixed to $\beta_{nn} = \alpha_{nn} = 0.4$. The host exchange rate β_{ni} with the invasive symbiont is fixed to $\beta_{ni} = 0.8$. The intrinsic growth rate of the host is fixed to $r_p = 0.5$. The dashed line corresponds to the biomass of the native pair host-symbiont alone. The red square corresponds to the critical values such that either the invader drives the system toward extinction (left square) or the invasive symbiont replaces the native symbiont (right square). The yellow square corresponds to the parasitic mutualistic nature of interactions between native host and invasive symbiont: parasitic symbiont (left square), parasitic host (right square).

D Analysis of the one symbiont and two competing hosts

We consider the case in which one native symbiont m is associated with 2 hosts (the native host p_n and the invasive host p_i) which compete between each other at a rate c. The corresponding differential equation system, is given by:

$$\begin{cases} \dfrac{dp_n}{dt} &= r_{p_n}\, p_n + \dfrac{Q_{p_n} m\, p_n}{\dfrac{p_n}{d} + \dfrac{p_i}{d} + m} - \mu_p p_n^2 - c_{p_n}\, p_i\,, \\ \dfrac{dp_i}{dt} &= r_{p_i}\, p_i + \dfrac{Q_{p_i} m\, p_i}{\dfrac{p_n}{d} + \dfrac{p_i}{d} + m} - \mu_p p_i^2 - c_{p_i}\, p_n \\ \dfrac{dm}{dt} &= \dfrac{m}{\dfrac{p_n}{d} + \dfrac{p_i}{d} + m}\,(Q_{m_n} p_n + Q_{m_i} p_i) - \mu_m m^2\,. \end{cases}$$

The hosts are either obligate or facultative mutualists ($r_{p_n} \geq 0$ and $r_{p_i} \geq 0$). The native host and the native symbionts are mutualistic, while the invasive host and the native symbiont might be either parasitic or mutualistic. In particular their exchange rates are given by

$$\begin{cases} Q_{p_n} = q_{hp}\dfrac{\alpha_{nn}}{d} - q_{cp}\beta_{nn} > 0 \\ Q_{m_n} = q_{cm}\beta_{nn} - q_{hm}\dfrac{\alpha_{nn}}{d} > 0 \end{cases} \quad \text{and} \quad \begin{cases} Q_{p_i} = q_{hp}\dfrac{\alpha_{ni}}{d} - q_{cp}\beta_{in}\,, \\ Q_{m_i} = q_{cm}\beta_{in} - q_{hm}\dfrac{\alpha_{ni}}{d}\,. \end{cases}$$

D.1 Steady state existence

To compute the steady state, we define the two following vectors $\mathbf{Q}_p$, $\mathbf{Q}_m$ of net gain and the competition matrix $\mathbf{C}_m$

$$\mathbf{Q}_p = \begin{pmatrix} Q_{p_n} \\ Q_{p_i} \end{pmatrix} \text{ and } \mathbf{Q}_m = \begin{pmatrix} Q_{m_n} & Q_{m_i} \end{pmatrix} \text{ and } \mathbf{C}_p = \begin{pmatrix} \mu_p & c \\ c & \mu_p \end{pmatrix},$$

The competition matrix can be reformulate as follows $\mathbf{C}_p = (\mu_p - c)I + c\mathbf{1}$, where $\mathbf{1}$ is the matrix full of 1 and I is the identity matrix. Thus the matrix $\mathbf{C}_p$ is invertible if and only if

$$\mu_p \neq c.$$

and its inverse satisfies

$$\mathbf{C}_p^{-1} = \frac{1}{\mu_p - c} I - \frac{c}{(\mu_p - c)(\mu_p + c)} \mathbf{1}\,.$$

We also define the two quantities: the free-symbiont equilibrium of coexisting hosts $\mathbf{p}_0$ and the total biomass of the system S;

$$\mathbf{p}_0 = \mathbf{C}_p^{-1} \begin{pmatrix} r_{p_n} \\ r_{p_i} \end{pmatrix} \text{ and } S = \frac{p_n}{d} + \frac{p_i}{d} + m.$$

Let us remark that the components of $\mathbf{p}_0$ are all positive, if and only if

$$c_p \leq \mu_p.$$

We immediately recover that if competition between hosts is too strong, coexistence of hosts is not possible.

Coexistence steady state A positive steady state (p_n, p_i, m) will satisfy the following problem:

$$\frac{1}{S}\mathbf{Q}_p m = \mathbf{C}_p \mathbf{p} - \mathbf{C}_p \mathbf{p}_0 \text{ and } \frac{1}{S}\mathbf{Q}_m \mathbf{p} = \mu_m m\,.$$

Combining the two systems, we obtain:

$$\frac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m} m = S^2 m - S \frac{\mathbf{Q}_m}{\mu_m} \mathbf{p}_0 \text{ and } \frac{\mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{Q}_m}{\mu_m} \mathbf{p} = S^2 \left(\mathbf{p} - \mathbf{p}_0\right)\,.$$

We can reformulate the system as follows:

$$(S^2 I - \mathbf{A})\mathbf{p} = S^2 \mathbf{p}_0 \text{ and } m = \frac{S q_0}{S^2 - \dfrac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m}}\,,$$

where $\mathbf{A} = \dfrac{\mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{Q}_m}{\mu_m}$, and $q_0 = \dfrac{\mathbf{Q}_m}{\mu_m} \mathbf{p}_0$.

Observing that $\mathrm{Tr}(\mathbf{A}) = \dfrac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m}$ and $\mathbf{A}^k = \left(\dfrac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m}\right)^{k-1} \mathbf{A}$ for any $k \geq 2$, we

deduce that

$$
\begin{aligned}
(S^2 I - \mathbf{A})^{-1} &= \frac{1}{S^2}\left(I - \frac{\mathbf{A}}{S^2}\right)^{-1} = \frac{1}{S^2}\sum_{k\geq 0}\left(\frac{\mathbf{A}}{S^2}\right)^k \\
&= \frac{1}{S^2}\left(I + \sum_{k\geq 1}\left(\frac{1}{S^2}\frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m}\right)^k \mathbf{A}\right) \\
&= \frac{1}{S^2}\left(I + \frac{\mathbf{A}}{S^2 - \frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m}}\right) = \frac{S^2 I + \left(\mathbf{A} - \frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m} I\right)}{S^2\left(S^2 - \frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m}\right)}.
\end{aligned}
$$

We can compute $\mathbf{p}$ as follows

$$
\mathbf{p} = (S^2 I - \mathbf{A})^{-1} S^2 \mathbf{p}_0 = \frac{S^2\mathbf{p}_0 + \left(\mathbf{A} - \frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m} I\right)\mathbf{p}_0}{\left(S^2 - \frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m}\right)}.
$$

Using the definition of S, we show that S is the positive root of the following third order polynomial

$$
S^3 - \frac{\mathbf{e}\mathbf{p}_0}{d}S^2 - \left(\frac{\mathbf{Q}_m}{\mu_m}\mathbf{p}_0 + \frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m}\right)S - \mathbf{e}\left(\frac{\mathbf{C}_p^{-1}\mathbf{Q}_p\mathbf{Q}_m}{\mu_m} - \frac{\mathbf{Q}_m\mathbf{C}_p^{-1}\mathbf{Q}_p}{\mu_m} I\right)\frac{\mathbf{p}_0}{d}.
$$

D.2 Parasitic versus mutualistic behaviour of host and symbiont

We here investigate the different nature of the interactions between two hosts (a native and an invasive one) and a symbiont, when the symbiont is initially associated with a native host, that can competes with the invasive host.

Parasitic symbiont. A symbiont associated with a native mutualistic host can be parasitic or pathogenic to an invasive host, that competes with the native host. It occurs when the exchange rate β_{in} is too large (rightmost yellow square Fig. D.2).

Pathogenic host If the host is too parasitic, $Q_{m_i} + Q_{m_n} < 0$ that corresponds to a low β_{in}, then invasive host drives the native symbiont toward extinction (leftmost red square in Fig.D.2).

Mutualistic/parasitic invasive host. When exchange rate β_{in} increases but remains low, then the invasive host is still parasitic with the symbiont as its biomass remains low until it becomes larger than its biomass at equilibrium with its native host alone. The mutualistic/parasitic threshold is represented by the leftmost yellow square in Fig; D.2.

Substitution of native host with invasive host. The invasive host may replace the native host when it gain competitive advantage from the native symbiont. It corresponds to the region between the two rightmost red square in Fig.D.2.

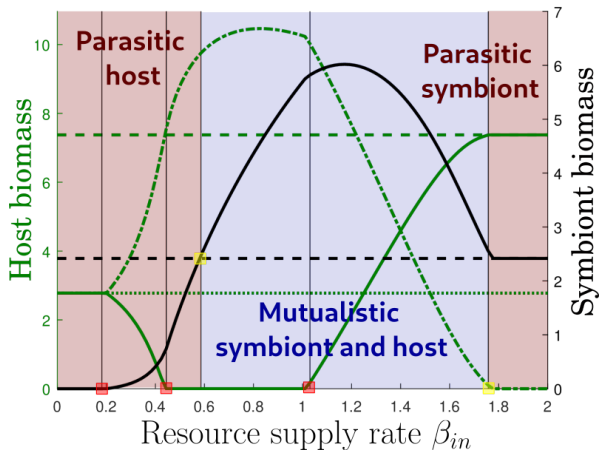


Fig. D.2: Parasitic or mutualistic invasive host and native symbiont. Evolution of the native host (solid green curve), invasive host (dashed green curve) and symbiont (solid black curve) biomass at equilibrium defined by (10), with respect to the exchange rate β_{in} of the invasive host to the native symbiont. The exchange rates between native pair are fixed to $\beta_{nn} = \alpha_{nn} = 0.4$. The symbiont exchange rate α_{ni} with the invasive host is fixed to $\alpha_{ni} = 0.8$. The host intrinsic growth rates are fixed to $r_p = 0.5$. The dashed line corresponds to the biomass of the native host-symbiont pair alone. The red squares correspond to the critical values such that the invader host drives the symbiont toward extinction (leftmost square), the invasive host replaces the native host (between the middle and rightmost squares). The yellow squares correspond to the parasitic mutualistic nature of interactions between native host and invasive symbiont: parasitic host (left square), parasitic symbiont (right square).

E Analysis of the different interaction scenarios

We consider here the main system (1) consisting of a native host associated with its native symbiont and an invasive host with its invasive symbiont. As in the main text, we assume that both the native host and the invasive host exchange nutrients with their respective symbionts at similar rates, i.e., $\alpha_{nn} = \alpha_{ii} = \alpha > 0$ and $\beta_{nn} = \beta_{ii} = \beta > 0$. Furthermore, we assume that the native pair and the invasive pair are mutualistic, that is their net gain Q_m and Q_p are positive:

$$Q_p = q_{hp}\frac{\alpha}{d} - q_{cp}\beta > 0 \quad \text{and} \quad Q_m = q_{cm}\beta - q_{hm}\frac{\alpha}{d} > 0\,.$$

In contrast, the exchange between native and invasive species may vary depending on the scenario: (1) no interactions between invasive and native species, (2)-(3) mutualistic interactions between invasive and native species, (4)-(7) parasitic interactions between invasive and native species (either parasitic host or parasitic symbiont), (see Table A.2 and Fig. 3 for details on the scenarios). The net gain resulting from the interaction between the native and invasive Q_m and Q_p will take the following values depending on the scenario

$$Q_p = \begin{cases} 0 & \text{neutral } (1) \\ q_p^- = -q_{cp}\beta < 0 & \text{parasitic symbiont } (4)-(6) \\ Q_p = q_{hp}\dfrac{\alpha}{d} - q_{cp}\beta > 0 & \text{mutualistic host and symbiont } (2)-(3) \\ q_p^+ = q_{hp}\dfrac{\alpha}{d} > Q_p > 0 & \text{parasitic host } (5)-(7) \end{cases}$$

and

$$Q_m = \begin{cases} 0 & \text{neutral } ① \\ q_m^+ = q_{cm}\beta > Q_m > 0 & \text{parasitic symbiont } ④ - ⑥ \\ Q_m = q_{cm}\beta - q_{hm}\dfrac{\alpha}{d} > 0 & \text{mutualistic host and symbiont } ② - ③ \\ q_m^- = -q_{hm}\dfrac{\alpha}{d} < 0 & \text{parasitic host } ⑤ - ⑦ \end{cases}$$

The model of Eq. (1) can be written as:

$$\begin{cases} \dfrac{dp_n}{dt} &= r_{p_n}p_n + \dfrac{p_n}{\dfrac{p_n}{d} + \dfrac{p_i}{d} + m_n + m_i}(m_nQ_p + m_iQ_{p_{ni}}) - \mu_p p_n^2 - c_p p_i p_n \,, \\ \dfrac{dm_n}{dt} &= \dfrac{m_n}{\dfrac{p_n}{d} + \dfrac{p_i}{d} + m_n + m_i}(p_nQ_m + p_iQ_{m_{in}}) - \mu_m m_n^2 - c_m m_i m_n \,, \\ \dfrac{dp_i}{dt} &= r_{p_i}p_i + \dfrac{p_i}{\dfrac{p_n}{d} + \dfrac{p_i}{d} + m_n + m_i}(m_iQ_p + m_nQ_{p_{in}}) - c_p p_n p_i - \mu_p p_i^2 \,, \\ \dfrac{dm_i}{dt} &= \dfrac{m_i}{\dfrac{p_n}{d} + \dfrac{p_i}{d} + m_n + m_i}(p_iQ_m + p_nQ_{m_{ni}}) - c_m m_n m_i - \mu_m m_i^2 \,. \end{cases} \tag{11}$$

For our analysis, it will be useful to define the two exchange matrices $\mathbf{Q}_p$ and $\mathbf{Q}_m$:

$$\mathbf{Q}_p = \begin{pmatrix} Q_p & Q_{p_{ni}} \\ Q_{p_{in}} & Q_p \end{pmatrix} \text{ and } \mathbf{Q}_m = \begin{pmatrix} Q_m & Q_{m_{in}} \\ Q_{m_{ni}} & Q_m \end{pmatrix},$$

One can remark that the interactions between the native host and the invasive symbiont are described by the couple $(Q_{p_{ni}}, Q_{m_{ni}})$, while the interaction between the invasive host and the native symbiont corresponds to $(Q_{p_{in}}, Q_{m_{in}})$.

We also define the two competition matrices $\mathbf{C}_p$ and $\mathbf{C}_m$:

$$\mathbf{C}_p = \begin{pmatrix} \mu_p & c_p \\ c_p & \mu_p \end{pmatrix} \text{ and } \mathbf{C}_m = \begin{pmatrix} \mu_m & c_m \\ c_m & \mu_m \end{pmatrix},$$

and the quantity $S = \dfrac{p_n}{d} + \dfrac{p_i}{d} + m_n + m_i$.

Then, using the notation $\mathbf{p} = (p_n, p_i)$, $\mathbf{m} = (m_n, m_i)$, and $\mathbf{r}_p = (r_{p_1}, r_{p_2})$, the system (11) can be reformulated as

$$\mathbf{p}' = \mathbf{p} \cdot \left(\mathbf{r}_p + \frac{\mathbf{Q}_p\mathbf{m}}{S} - \mathbf{C}_p\mathbf{p}\right)$$
$$\mathbf{m}' = \mathbf{m} \cdot \left(\frac{\mathbf{Q}_m\mathbf{p}}{S} - \mathbf{C}_m\mathbf{m}\right).$$

E.1 Steady states of the system

In order to understand the outcome of the interactions between native and invasive species, we first describe the possible steady states of the system.

E.1.1 Exclusion steady states consisting of one host and one symbiont

In our system, the steady state that comprises only one host and one symbiont always exists. Therefore there are four possible exclusion steady states:

$$\begin{array}{ll} (p_n^*, m_n^*, 0, 0) & \text{native pair} \\ (0, 0, p_i^*, m_i^*) & \text{invasive pair} \\ (p_n^*, 0, 0, m_i^*) & \text{mixed pair, invasive symbiont with native host} \\ (0, m_n^*, p_i^*, 0) & \text{mixed pair, invasive host with native symbiont} \end{array} \tag{12}$$

Due to our choice of parameters (i.e., with α_{nn}, α_{ii}, β_{nn} and β_{ii} large enough), the steady state with only native species or only invasive species always exist. However, the mixed steady states composed of either a native host with an invasive symbiont, or an invasive host with a native symbiont, only exist when the cross-species are both mutualistic, that corresponds to scenarios 2-3 (see section B.1).

E.1.2 Inclusion steady states consisting of one host and two symbionts

The inclusion steady state that we consider in this section corresponds to the case where one host integrates the symbiont from the other host and excludes the other host. In our system, we have two possible steady states of this form

$$(p_n, 0, m_n, m_i) \text{ and } (0, p_i, m_n, m_i) \text{ symbiont inclusion state.}$$

These equilibrium exist if the **competition between the symbionts is weak** and symbionts are not too parasitic (see section C.1).

E.1.3 Inclusion steady states consisting of two hosts and one symbiont

This inclusion steady state corresponds to the case where one symbiont supports the two hosts and excludes the other symbiont. In our system, we have two possible steady states of this form

$$(p_n, p_i, m_n, 0) \text{ and } (p_n, p_i, 0, m_i) \text{ host inclusion state.}$$

These equilibrium exist if **competition between hosts is weak** and the remaining symbiont is mutualistic and the host are not too parasitic (see section D.1).

E.1.4 Coexistence steady state consisting of two hosts and two symbionts

The last possible equilibrium is the coexistence state where native and invasive species survive, that i s

$$(p_n, p_i, m_n, m_i) \text{ coexistence state.}$$

This steady state only exists when the **competition between symbionts and between hosts are weak**.

E.2 Outcome of the different interaction scenarios

We first investigate the outcome of the 7 scenarios under strong competition between symbionts and between hosts, that is

$$c_p > \mu_p \text{ and } c_m > \mu_m.$$

Then, we discuss scenarios 2 and 3, that corresponds to mutualistic host-symbiont interactions, under weak competition to show that inclusion steady state or even coexistence can occur.

E.2.1 Strong competition between hosts and symbionts

In this situation, only the exclusion equilibrium, defined in (12) can exist and their stability crucially depends on the interactions. To define this dependence more precisely, we compute

the Jacobian matrix of the steady state. For any of the four exclusion equilibrium, the jacobian takes the following form

$$J = \left(\begin{array}{c|c} J(p^*, m^*) & B \\ \hline 0 & I \end{array}\right)$$

where p^*, m^* stands for the positive biomass of host an symbiont at equilibrium, $J(p^*, m^*)$ is defined by (9) in section B.3 and B and I are 2×2 matrices, and I describes the interactions between the excluded host and symbiont and the surviving ones. From the analysis of Section B.3, we know that the matrix $J(p^*, m^*)$ has two negative eigenvalues. The matrix I is diagonal with coefficients that depends on the exclusion equilibrium as follows

Native pair $(p_n, m_n, 0, 0)$

$$I_{nn} = \begin{pmatrix} \dfrac{p_0}{S^2 - \dfrac{Q_p Q_m}{\mu_p \mu_m}} \left(\left(1 - \dfrac{c_p}{\mu_p}\right) S^2 - \dfrac{Q_p Q_m}{\mu_p \mu_m} \left(1 - \dfrac{Q_{p_{in}}}{Q_p}\right) \right) & 0 \\ 0 & \left(\dfrac{Q_{m_{ni}}}{Q_m} \mu_m - c_m \right) m_n \end{pmatrix}$$

Invasive pair $(0, 0, p_i, m_i)$

$$I_{ii} = \begin{pmatrix} \dfrac{p_0}{S^2 - \dfrac{Q_p Q_m}{\mu_p \mu_m}} \left(\left(1 - \dfrac{c_p}{\mu_p}\right) S^2 - \dfrac{Q_p Q_m}{\mu_p \mu_m} \left(1 - \dfrac{Q_{p_{ni}}}{Q_p}\right) \right) & 0 \\ 0 & \left(\dfrac{Q_{m_{in}}}{Q_m} \mu_m - c_m \right) m_i \end{pmatrix}$$

Mixed pair, invasive symbiont spillover, $(p_n, 0, m_i, 0)$

$$I_{ni} = \begin{pmatrix} \dfrac{p_0}{S^2 - \dfrac{Q_{p_{ni}} Q_{m_{ni}}}{\mu_p \mu_m}} \left(\left(1 - \dfrac{c_p}{\mu_p}\right) S^2 - \dfrac{Q_{p_{ni}} Q_{m_{ni}}}{\mu_p \mu_m} \left(1 - \dfrac{Q_p}{Q_{p_{ni}}}\right) \right) & 0 \\ 0 & \left(\dfrac{Q_m}{Q_{m_{ni}}} \mu_m - c_m \right) m_i \end{pmatrix}$$

Mixed pair, invasive host invasion, $(0, m_n, p_i, 0)$

$$I_{in} = \begin{pmatrix} \dfrac{p_0}{S^2 - \dfrac{Q_{p_{in}} Q_{m_{in}}}{\mu_p \mu_m}} \left(\left(1 - \dfrac{c_p}{\mu_p}\right) S^2 - \dfrac{Q_{p_{in}} Q_{m_{in}}}{\mu_p \mu_m} \left(1 - \dfrac{Q_p}{Q_{p_{in}}}\right) \right) & 0 \\ 0 & \left(\dfrac{Q_m}{Q_{m_{ni}}} \mu_m - c_m \right) m_n \end{pmatrix}$$

1 Native and invasive species do not share symbionts nor hosts. In this scenario, the cross-species exchange are null, that is $Q_{p_{in}} = Q_{p_{ni}} = 0 = Q_{m_{in}} = Q_{m_{ni}}$, and the exchange matrices $\mathbf{Q}_m$ and $\mathbf{Q}_p$ become

$$\mathbf{Q}_p = \begin{pmatrix} Q_p & 0 \\ 0 & Q_p \end{pmatrix} \quad \text{and} \quad \mathbf{Q}_m = \begin{pmatrix} Q_m & 0 \\ 0 & Q_m \end{pmatrix},$$

We deduce that the matrices I_{nn} and I_{ii} have negative coefficients, and the **exclusion steady states with either native or invasive species are stable**.

(2) Mutualistic association between native symbionts and invasive hosts. In this scenario, the exchange between native symbiont and invasive host are positive, that is $Q_{p_{ni}} = Q_p > 0$ and $Q_{m_{ni}} = Q_m > 0$, while the exchange between native host and invasive symbiont are null, that is $Q_{p_{in}} = 0 = Q_{m_{in}}$. The exchange matrices $\mathbf{Q}_m$ and $\mathbf{Q}_p$ become

$$\mathbf{Q}_p = \begin{pmatrix} Q_p & 0 \\ Q_p & Q_p \end{pmatrix} \text{ and } \mathbf{Q}_m = \begin{pmatrix} Q_m & Q_m \\ 0 & Q_m \end{pmatrix},$$

Under strong competition, we deduce that the matrices I_{nn}, I_{ii} and I_{ni} have negative coefficients, and the **exclusion steady states with either native or invasive species and the mixed pair with invasive host and native symbiont are stable**.

(3) Mutualistic association between native hosts and invasive symbionts. Similarly to previous scenario, the exchange between invasive symbiont and native host are positive, that is $Q_{p_{in}} = Q_p > 0$ and $Q_{m_{in}} = Q_m > 0$, while the exchange between invasive host and native symbiont are null, that is $Q_{p_{ni}} = 0 = Q_{m_{ni}}$. The exchange matrices $\mathbf{Q}_m$ and $\mathbf{Q}_p$ become

$$\mathbf{Q}_p = \begin{pmatrix} Q_p & Q_p \\ 0 & Q_p \end{pmatrix} \text{ and } \mathbf{Q}_m = \begin{pmatrix} Q_m & 0 \\ Q_m & Q_m \end{pmatrix},$$

Under strong competition, we deduce that the matrices I_{nn}, I_{ii} and I_{in} have negative coefficients, and the **exclusion steady states with either native or invasive species and the mixed pair with native host and invasive symbiont are stable**.

(4) Native symbionts are parasitic to invasive hosts. In this scenario, the native symbiont is parasitic to invasive host, that is $Q_{p_{in}} = q_p^- < 0$ and $Q_{m_{in}} = q_m^+ > Q_m > 0$, while the exchange between native host and invasive symbiont are null, that is $Q_{p_{ni}} = 0 = Q_{m_{ni}}$. The exchange matrices $\mathbf{Q}_m$ and $\mathbf{Q}_p$ become

$$\mathbf{Q}_p = \begin{pmatrix} Q_p & 0 \\ q_p^- & Q_p \end{pmatrix} \text{ and } \mathbf{Q}_m = \begin{pmatrix} Q_m & q_m^+ \\ 0 & Q_m \end{pmatrix},$$

Under strong competition, we deduce that the matrices I_{nn} have negative coefficients. The **exclusion equilibrium with native species is stable**

However, the matrix I_{ii} have a negative coefficient

$$(1 - c_p/\mu_p)\, S^2 - Q_p Q_m/(\mu_p \mu_m)\,(1 - Q_{p_{ni}}/Q_p) < 0$$

and possibly a positive coefficient, if the symbiont is really parasitic in the sense that

$$Q_{m_{in}} > \frac{c_m}{\mu_m} Q_m \;\Leftrightarrow\; \alpha_{ni} < \frac{q_{cm}}{q_{hm}} \beta_{in}\, d - \frac{c_m}{\mu_m} Q_m.$$

This inequality may be fulfilled if the symbiont is parasitic in the sense of definition of section B.2 and the invasive host is mutualistic enough to the symbiont. Otherwise, the native symbiont has to be really parasitic. Thus if the native symbiont is parasitic enough relative to the invasive host, the equilibrium with **invasive species is unstable**.

(5) Invasive hosts are parasitic to native symbionts. In this scenario, the invasive host is parasitic to native symbiont, that is $Q_{p_{in}} = q_p^+ > Q_p > 0$ and $Q_{m_{in}} = q_m^- < 0$, while the exchange between native host and invasive symbiont are null, that is $Q_{p_{ni}} = 0 = Q_{m_{ni}}$. The exchange matrices $\mathbf{Q}_m$ and $\mathbf{Q}_p$ become

$$\mathbf{Q}_p = \begin{pmatrix} Q_p & 0 \\ q_p^+ & Q_p \end{pmatrix} \text{ and } \mathbf{Q}_m = \begin{pmatrix} Q_m & q_m^- \\ 0 & Q_m \end{pmatrix},$$

Under strong competition, we deduce that the matrices I_{ii} have negative coefficients. The **exclusion equilibrium with invasive species is stable**.

However, the matrix I_{nn} have a negative coefficient $Q_{m_{in}}/Q_m - c_m/\mu_m < 0$ and possibly a positive coefficient, if the host is really parasitic in the sense that

$$Q_{p_{in}} > Q_p \left(1 + \left(\frac{c_p}{\mu_p} - 1\right) \frac{S^2}{\frac{Q_p Q_m}{\mu_p \mu_m}}\right) \Leftrightarrow \beta_{in} < \frac{q_{hp}}{q_{cp}} \frac{\alpha_{ni}}{d} - Q_p \left(1 + \left(\frac{c_p}{\mu_p} - 1\right) \frac{S^2}{\frac{Q_p Q_m}{\mu_p \mu_m}}\right)$$

Thus if the invasive host is parasitic enough relative to the native symbiont, the equilibrium with **native species is unstable**.

6 Invasive symbionts are parasitic to native hosts. This scenario is similar to the scenario 4. The **exclusion equilibrium with invasive species is stable** and if the invasive symbiont is parasitic enough relative to the native host, the equilibrium with **native species is unstable**.

7 Native hosts are parasitic to invasive symbionts. This scenario is similar to the scenario 5. The **exclusion equilibrium with native species is stable** and if the native host is parasitic enough relative to the invasive symbiont, the equilibrium with **invasive species is unstable**.

E.3 A simplified model on the proportion of native host and symbiont

In order to understand the outcome of the 7 scenario described in our manuscript, we will reformulate the problem by focusing on the proportion ϕ_p of native host and the proportion ϕ_m of native symbiont in the system, that are defined by

$$\phi_p = \frac{p_n}{p_n + p_i} \quad \text{and} \quad \phi_m = \frac{m_n}{m_n + m_i}$$

We also introduce the total biomass of the host $P = p_n + p_i$ and the total biomass of symbiont $M = m_n + m_i$. Let us remark that those quantities are related to S, $S = P/d + M$. Using the model (11), the proportions ϕ_p and ϕ_m satisfies the following dynamical system

$$\begin{cases} \phi_p' = \phi_p(1-\phi_p)\Big(\Big(\big(2Q_p - (Q_{p_{in}} + Q_{p_{ni}})\big)\phi_m - (Q_p - Q_{p_{ni}})\Big)\dfrac{M}{S} \\ \qquad\qquad + (c_p - \mu_p)(2\phi_p - 1)P\Big) \\ \phi_m' = \phi_m(1-\phi_m)\Big(\Big(\big(2Q_m - (Q_{m_{in}} + Q_{m_{ni}})\big)\phi_p - (Q_m - Q_{m_{in}})\Big)\dfrac{P}{S} \\ \qquad\qquad + (c_m - \mu_m)(2\phi_m - 1)M\Big) \end{cases} \tag{13}$$

Since M, P and S are not constant over time, the system is not autonomous and a simple phase plane won't explain the dynamics of (ϕ_p, ϕ_m). However, we know from the full system (11), that those quantities are always positive and bounded. Thus, we can expect that the phase plane when we fix M, P to a constant will explain the dynamics of the full system.

E.3.1 Steady states of the simplified system

Under the 7 scenarios (1)-(7), we assume that the competition between symbionts and hosts are strong ($c_m > \mu_m$ and $c_p > \mu_p$). Thus, the simplified model mainly contains trivial steady states corresponding to exclusion steady states of the full model

$(1,1)$	native pair
$(0,0)$	invasive pair
$(1,0)$	mixed pair, invasive symbiont spillover
$(0,1)$	mixed pair, invasive host invasion

Because the competition is strong, non trivial equilibrium will be unstable if they exist.

E.3.2 Phase plane of the simplified model for the 7 scenarios

The phase plane of the simplified model of Eq. (13) are provided in Fig. E.1, and can help us understand expected dynamics occurring in scenarios 1-7. A schematic representation of the outcomes of these scenarios is also provided in Fig. 3, in the main manuscript.

1 Native and invasive species do not share symbionts nor hosts. In this scenario, we expect the equilibrium to reach either the (p_n^*, m_n^*,0,0) or the (0,0,p_i^*,m_i^*) steady state, as shown in Fig. E.1 1. Which steady state is reached, depends on the initial conditions and model parameters, determining the size of the basin of attraction of each steady state. This situation of bistability is also discussed in scenario 1 of the result section and illustrated in Fig. 3(a).

2 Mutualistic association between native symbionts and invasive hosts. Three steady states are possible, following the formation of novel mutualistic associations between invasive hosts and invasive symbionts, namely: (p_n^*,m_n^*,0,0), (0,m_n^*,p_i^*,0), and (0,0,p_i^*,m_i^*). A schematic representation of this scenario is provided in Fig. 3(b). Note that the steady state (0,m_n^*,p_i^*,0) can be reached through different routes, in orange and yellow in Fig. E.1 2. A route in which the density of native symbionts is increased at first (in orange) and a route in which the density of invasive hosts is increased at first (in yellow). These two routes corresponds to the center left and center right pathways in Fig. 3(b).

3 Mutualistic association between native hosts and invasive symbionts. Three steady states can be observed following the formation of novel associations between native hosts and invasive symbionts: (p_n^*,m_n^*,0,0), (p_n^*,0,0,m_i^*), and (0,0,p_i^*,m_i^*), where the steady state (0,m_n^*,p_i^*,0) can be reached through different routes, in orange and yellow in Fig. E.1 3. A schematic representation of this scenario is provided in Fig. 3(c). The center left and right pathway in this figure correspond on the orange and yellow pathways in the phase plane. A route in which the density of native symbionts is increased at first (in orange) and a route in which the density of invasive hosts is increased at first (in yellow). These two routes corresponds to the center left and center right pathways in Fig. 3(b).

4 Native symbionts are parasitic to invasive hosts, and 7 Native hosts are parasitic to invasive symbionts. In these cases, only one steady state (p_n^*,m_n^*, 0, 0) is stable, as the exclusion of invasive species (either hosts or symbionts) leads to the extinction of their invasive partner, as seen in Fig. E.1 4 and 7 and in Fig. 3(a).

5 Invasive hosts are parasitic to native symbionts, and 6 Invasive symbionts are parasitic to native hosts. In these cases, the only stable steady state is (0,0,p_i^*,m_i^*), as shown in Fig. E.1 5 and 6 and in Fig. 3(a). This is because the exclusion of native hosts or symbionts, due to exploitation by invasive species, leads as well to the exclusion of the native mutualistic partner.

F Multiple hosts and multiple symbionts model

Our framework can be extended to consider multiple hosts and symbionts. If we consider M competing hosts exchanging resources with N competing symbionts, we obtain:

$$\begin{cases} \dfrac{dp_j}{dt} & = r_{p_j} p_j + \dfrac{p_j}{\dfrac{\sum_j p_j}{d} + \sum_i m_i} \sum_i m_i Q_{p_{ij}} - \mu_p p_j^2 - c_p \sum_{k \neq j} p_k \,, \quad \text{for} \quad j = 1, ..., M \,, \\ \dfrac{dm_i}{dt} & = \dfrac{m_i}{\dfrac{\sum_j p_j}{d} + \sum_i m_i} \sum_j p_j Q_{m_{ji}} - \mu_m m_i^2 - c_m \sum_{l \neq i} m_l \,, \quad \text{for} \quad i = 1, ..., N \,, \end{cases}$$

where $Q_{p_{ij}}$ is the effect of symbiont i on host j and $Q_{m_{ji}}$ is the effect of host j on symbiont i. These are defined for any $i \in \{1, \ldots, N\}$ and $j \in \{1, \ldots, M\}$ by

$$Q_{p_{ij}} = q_{hp} \frac{\alpha_{ji}}{d} - q_{cp} \beta_{ij} \quad \text{and} \quad Q_{m_{ij}} = q_{cm} \beta_{ji} - q_{hm} \frac{\alpha_{ij}}{d} \,.$$

An analysis of this system is beyond the scope of this paper, and will be left to future work.

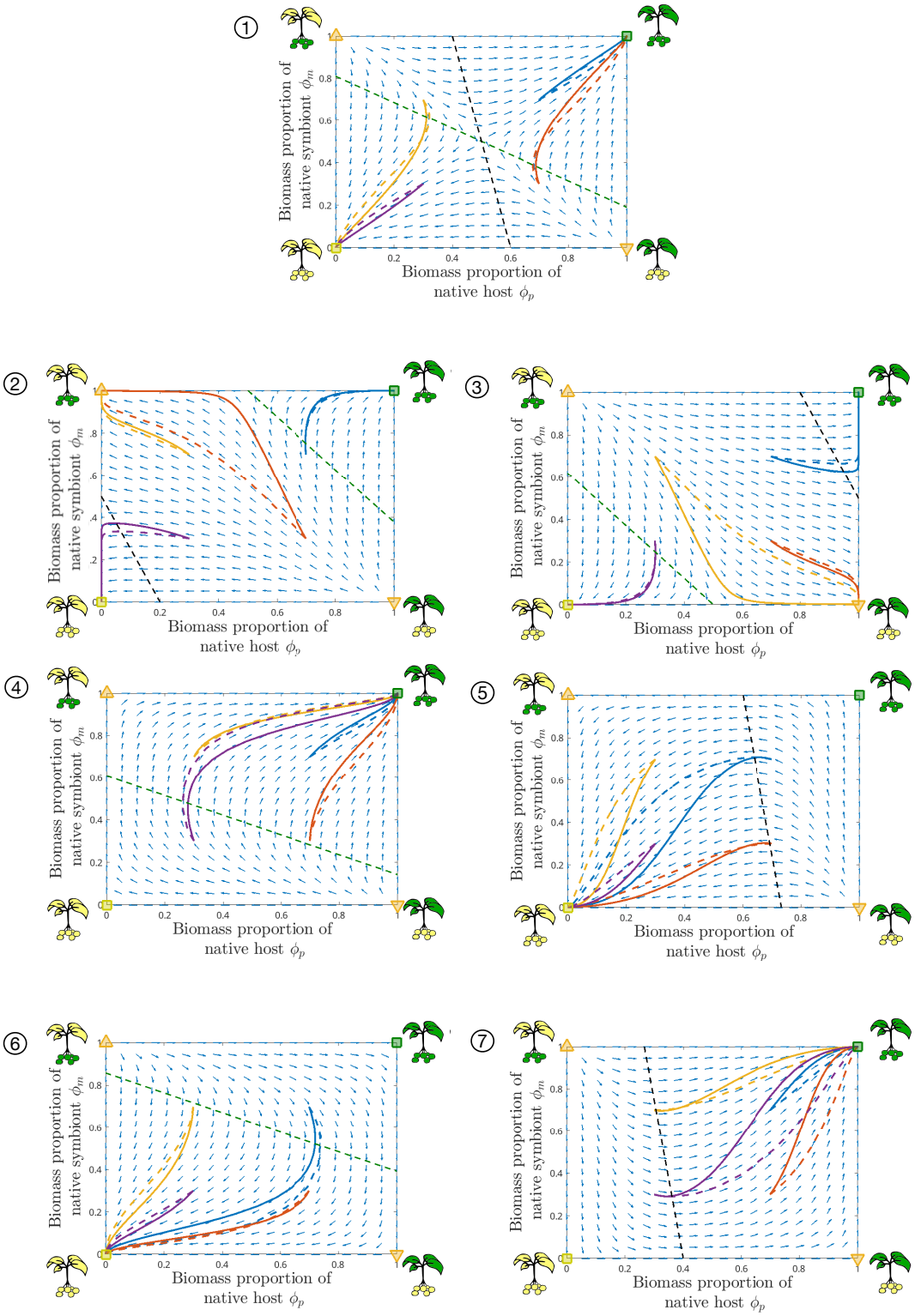


Fig. E.1: Phase plane of the approximation model (13). The green square corresponds to the exclusion equilibrium with native species, the yellow square corresponds to the exclusion equilibrium with invasive species, and the orange triangles correspond to mixed pair equilibria. Shown are 4 trajectories of the full system (11) (solid curves) and the approximated model (dashed curves). The straight dashed lines correspond to the nullclines of the system, and the arrows are the approximation of the flow (13).