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► **To cite this version:**

Maria Martignoni, Jimmy Garnier, Rebecca Tyson, Keith Harris, Oren Kolodny. Toward a unified theory of microbially-mediated invasion. 2025. hal-04440495v2

HAL Id: hal-04440495

<https://hal.science/hal-04440495v2>

Preprint submitted on 30 Jan 2025

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Toward a unified theory of microbially-mediated invasion

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January 30, 2025

Abstract

Biological invasions pose major ecological and economic threats, and extensive research has been dedicated to understanding and predicting their dynamics. Most studies focus on the biological invasion of single species, and only in recent years has it been realized that multi-species interactions that involve native and invasive host species and their microbial symbionts can play important roles in determining invasion outputs. A theoretical framework that treats these interactions and their impact is lacking. Here we offer such a framework and use it to explore possible dynamics that may emerge from the horizontal sharing of native and non-native microbial symbionts among native and non-native host individuals and species. Thus, for example, invasive plants might benefit from native mycorrhizal networks in the soil, or might be particularly successful if they carry with them parasites to which competing native hosts are susceptible. On the other hand, invasion might be hindered by native parasites that spread from native to invasive individuals. The mathematical framework that we lay out in this study provides a new mechanistic, cohesive, and intuition-enhancing tool for theoretically exploring the ways by which the subtleties of the relationships between hosts and microbes may affect invasion dynamics. We identify multiple pathways through which microbes can facilitate (or prevent) host invasion, microbial invasion, and the invasion of both hosts and their co-introduced microbes. We disentangle invasion outcomes and highlight modalities of ecological dynamics that have so far not been considered in invasion biology. Our work sets the foundations for invasion theory that includes a community-level view of invasive and native hosts as well as their microbial symbionts.

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Statements and declarations

- The authors have no competing interests to declare that are relevant to the content of this article.
- All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.
- The authors have no financial or proprietary interests in any material discussed in this article.
- This study did not require any human involvement, and no human data was taken during the study
- 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>).
- Fundings: MMM was funded by the Azrieli Foundation. OK was funded by the Israel Science Foundation (ISF) (grant number 1826/20), the Gordon and Betty Moore Foundation, the United States-Israel Binational Science Foundation (BSF), and The Minerva Center for the Study of Population Fragmentation. RCT was funded by the Natural Sciences and Engineering Research Council (NSERC) of Canada Discovery Grants Program, grant number RGPIN-2022-03589, and the University of British Columbia Okanagan Institute for Biodiversity, Resilience, and Ecosystem Services. JG was funded by ModEcoEvo project funded by the Université Savoie Mont-Blanc and the ANR project ReaCh (ANR-23-CE40-0023-01).
- Author’s contributions: MMM: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing - Original Draft, Writing - Review & Editing. JG: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing - Review & Editing. RT: Conceptualization, Methodology, Writing - Review & Editing. KH: Results visualization on modelRxiv. OK: Conceptualization, Methodology, Writing - Review & Editing. All authors agree with the present manuscript.

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

1 Biological invasion is often regarded as invasion by a single species. However, organisms live
2 in symbiosis with a rich and diverse collection of microbial symbionts that are an essential
3 component of their host’s fitness and reproductive success (Fitzpatrick et al., 2020; Compant
4

5 [et al., 2019](#)). Microbial communities can encompass mutualistic, commensal, and parasitic
6 (or pathogenic) symbionts that benefit or harm the host to different extents. The fitness of
7 these microbial symbionts, in turn, depends on their association with host partners, such that
8 the fates of hosts and symbionts are intrinsically linked, and so are the possibilities for hosts
9 and symbionts to successfully establish and persist in a new environment. For example, the
10 formation of novel associations between invasive plants and pre-existing native mycorrhizal
11 networks can facilitate the establishment of an introduced host population and its expansion
12 into a new range ([Dawkins and Esiobu, 2016](#); [Parepa et al., 2013](#); [Moeller et al., 2015](#)). The
13 spread of introduced symbionts can also be facilitated by native hosts ([Díez, 2005](#); [Wolfe and](#)
14 [Pringle, 2012](#); [Dickie et al., 2016](#)), where the spread of introduced pathogens may cause the
15 emergence of disease in native species and lead to their competitive exclusion ([Panzavolta](#)
16 [et al., 2021](#); [Santini et al., 2013](#); [Grünwald et al., 2012](#); [Schuchert et al., 2014](#)). In other cases,
17 host-symbiont interactions can provide resilience to native communities. For instance, host
18 invasiveness may be decreased by a reduction in the abundance of their mutualistic symbionts
19 ([Zenni and Nuñez, 2013](#); [Catford et al., 2009](#)), or by the transmission of pathogenic agents
20 from native to invasive hosts ([Mordecai, 2013](#); [Flory and Clay, 2013](#)).

21 Awareness of the importance of host-symbiont associations in dynamics of host and mi-
22 crobial invasion is growing rapidly, and so are attempts at developing conceptual frameworks
23 to understand the impact of parasitic or mutualistic host-symbiont associations on invasion
24 outcomes ([Dickie et al., 2017](#); [Amsellem et al., 2017](#); [Dunn and Hatcher, 2015](#); [Médoc et al.,](#)
25 [2017](#); [Mitchell et al., 2006](#); [Nuñez et al., 2009](#); [Dickie et al., 2017](#)). However, more studies
26 are needed to fully understand the impact that multi-species interactions that involve native
27 and invasive species and their microbial symbionts may have on invasion dynamics. From a
28 theoretical point of view, ecological population modelling has mostly studied the range ex-
29 pansion and invasion dynamics of either parasite ([White et al., 2018](#); [Gubbins et al., 2000](#)),
30 or host populations ([Lewis et al., 2016](#)), rarely accounting for the role that host-symbiont
31 feedback can have on the invasion dynamics. Even in the few instances in which these feed-
32 backs were considered ([Bever et al., 1997](#); [Yamauchi et al., 2011](#); [Jack et al., 2017](#); [Martignoni](#)
33 [and Kolodny, 2023](#); [Kandlikar et al., 2019](#)), studies mostly unilaterally discussed how diver-
34 sity and fitness of the host population can be mediated by microbial communities and not
35 vice-versa. Host and symbiont fitness is interdependent: symbionts can influence the growth
36 and coexistence of host populations, and changes in host populations will, in turn, influence
37 fitness and diversity in symbiont communities, all of which can affect competitive dynamics
38 between hosts and between symbionts.

39 Theoretical insights into the stability and resilience of mutualistic and parasitic commu-
40 nities against invasion have been provided by network theory. These approaches have mainly
41 focused on relating community invasiveness to network properties, such as nestedness, or con-
42 nectivity ([Campbell et al., 2012](#); [Bastolla et al., 2009](#); [Rohr et al., 2014](#); [Vacher et al., 2010](#)),
43 where network structure is based on trait-based approaches considering how trait differences
44 and similarities in the invaded and invading communities may affect interaction strength ([Mi-](#)
45 [noarivelo and Hui, 2016a](#); [Hui et al., 2016](#); [Minoarivelo and Hui, 2016b](#); [Schleuning et al.,](#)
46 [2015](#); [Runghen et al., 2021](#)). These studies can help identify common features of mutualistic
47 or host-parasite networks, and test hypotheses regarding the relationship between structure
48 and community dynamics ([Valdovinos, 2019](#); [Bascompte and Olesen, 2015](#)). However, par-
49 ticularly for the case of mutualistic networks, analyses have been performed on communities
50 of free-living species, such as pollination or seed-dispersal mutualisms ([Bascompte and Jor-](#)
51 [dano, 2013](#)), whose dynamics may differ from what is observed when microbial symbionts
52 are obligate mutualists. Additionally, theoretical results are largely based on Lotka-Volterra
53 equations that may lead to inaccurate predictions due to their unrealistic biological assump-
54 tions, 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 ecological communities of hosts and their symbionts (herein referred to as '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 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 symbionts. 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 may 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); Goedknecht 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 symbionts interact by exchanging resources necessary for each other's growth. For example, in the case of the mycorrhizal symbiosis, the host plant provides 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, as described by the F_m functions below. The transfer of resources from symbionts to hosts increases host biomass and decreases symbiont biomass, as described by the F_p functions below. We consider hosts to be facultative mutualists, and capable of some growth in the absence of the symbionts (with intrinsic growth

101 rate quantified by the parameter r_p), while symbionts are obligate mutualists and can not
 102 grow in the absence of a host. We then extend this model to include interactions between an
 103 invasive host population (with biomass p_i) and its invasive symbiont community (with biomass
 104 m_i). We consider that native symbiont may exchange resources with native hosts, and invasive
 105 symbiont may exchange resources with native hosts. Competition between native and invasive
 106 hosts (c_p parameters) and between native and invasive symbionts (c_m parameters), may reduce
 107 their abundance, e.g., due to competition for host colonization between symbionts (Engelmoer
 108 et al., 2014; Smith et al., 2018), or due to host competition for light or other external resources
 109 (Craine and Dybzinski, 2013).

We obtain the following equations:

$$\frac{dp_n}{dt} = r_{p_n} p_n + F_{p_n}(p_n, m_n, p_i, m_i) - c_{p_{in}} p_n p_i - \mu_{p_n} p_n^2, \quad (1a)$$

$$\frac{dm_n}{dt} = F_{m_n}(p_n, m_n, p_i, m_i) - c_{m_{in}} m_n m_i - \mu_{m_n} m_n^2, \quad (1b)$$

$$\frac{dp_i}{dt} = r_{p_i} p_i + F_{p_i}(p_n, m_n, p_i, m_i) - c_{p_{ni}} p_n p_i - \mu_{p_i} p_i^2, \quad (1c)$$

$$\frac{dm_i}{dt} = F_{m_i}(p_n, m_n, p_i, m_i) - c_{m_{ni}} m_n m_i - \mu_{m_i} m_i^2, \quad (1d)$$

with functions F_{p_n} , F_{p_i} , F_{m_n} , and F_{m_i} defined as

$$F_{p_n} = \underbrace{q_{hp_n} p_n \left(\frac{\alpha_{nn} m_n + \alpha_{in} m_i}{p_n/d + p_i/d + m_n + m_i} \right)}_{\text{supply from } m_n \text{ and } m_i} - \underbrace{q_{cp_n} p_n \left(\frac{\beta_{nn} m_n + \beta_{ni} m_i}{p_n + p_i + dm_n + dm_i} \right)}_{\text{supply to } m_n \text{ and } m_i}, \quad (2a)$$

$$F_{m_n} = \underbrace{q_{cm_n} m_n \left(\frac{\beta_{nn} p_n + \beta_{in} p_i}{p_n + p_i + dm_n + dm_i} \right)}_{\text{supply from } p_n \text{ and } p_i} - \underbrace{q_{hm_n} m_n \left(\frac{\alpha_{nn} p_n + \alpha_{ni} p_i}{p_n/d + p_i/d + m_n + m_i} \right)}_{\text{supply to } p_n \text{ and } p_i}, \quad (2b)$$

$$F_{p_i} = \underbrace{q_{hp_i} p_i \left(\frac{\alpha_{ii} m_i + \alpha_{ni} m_n}{p_n/d + p_i/d + m_n + m_i} \right)}_{\text{supply from } m_i \text{ and } m_n} - \underbrace{q_{cp_i} p_i \left(\frac{\beta_{ii} m_i + \beta_{in} m_n}{p_n + p_i + dm_n + dm_i} \right)}_{\text{supply to } m_i \text{ and } m_n}, \quad (2c)$$

$$F_{m_i} = \underbrace{q_{cm_i} m_i \left(\frac{\beta_{ii} p_i + \beta_{ni} p_n}{p_n + p_i + dm_n + dm_i} \right)}_{\text{supply from } p_i \text{ and } p_n} - \underbrace{q_{hm_i} m_i \left(\frac{\alpha_{ii} p_i + \alpha_{in} p_n}{p_n/d + p_i/d + m_n + m_i} \right)}_{\text{supply to } p_i \text{ and } p_n}. \quad (2d)$$

110 A schematic representation of this model is provided in Fig. 1(a). A table with a brief
 111 description of model parameters is provided in SI A.

112 The transfer of resources from symbionts to hosts and from hosts to symbionts is quanti-
 113 fied by the α_{jk} and β_{jk} parameters respectively, with subindex j representing the supplying
 114 species (n for native, or i for invasive), and subindex k representing the receiving species.
 115 These parameters may represent particular traits in the receiving and supplying species, that
 116 quantify the resource exchange capacity of each one. For instance, microbes that provide lots
 117 of phosphorus to host plants and take lots of carbon from host plants are represented by large
 118 α_j and β_j parameters. Additionally, native and invasive species can differ in their intrinsic
 119 growth rate (parameters r_{p_j} , $j = n, i$), in their efficiency at converting the resource received
 120 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
 121 which resources need to be diverted into maintenance of the existing biomass (parameters μ_{p_j}
 122 and μ_{m_j} , with $j = n, i$).

123 To explore the effect of host-symbiont association on invasion dynamics, we consider that
 124 parameters α_{in} , α_{ni} , β_{in} and β_{ni} can be zero or positive, depending on whether or not re-
 125 source exchange between invasive symbionts/hosts and native hosts/symbionts is occurring.

126 If invasive hosts exchange nutrients with native symbionts, parameters α_{ni} (quantifying the
 127 resource supply from native symbionts to invasive hosts) and β_{in} (quantifying the resource
 128 supply from invasive hosts to native symbionts) will assume positive values. The relationship
 129 between how much a host receives from its associated symbionts (which depends on α paramete-
 130 ters) and how much a host gives to its associated symbionts (which depends on β paramete-
 131 rs) per unit time determines whether a host-symbiont relationship is mutualistic or parasitic for
 132 the host or the symbiont population (see Fig. 1b). Generally, the relationship is parasitic for
 133 the host population if $\alpha \ll \beta$, and parasitic for the symbiont community if $\beta \ll \alpha$, while the
 134 interaction is mutualistic for both hosts and symbionts, for $\alpha \simeq \beta$. A detailed explanation of
 135 the quantitative criteria used to understand whether the exchange is mutualistic or parasitic
 136 is provided below in the ‘Model analysis and scenarios of interest’ section.

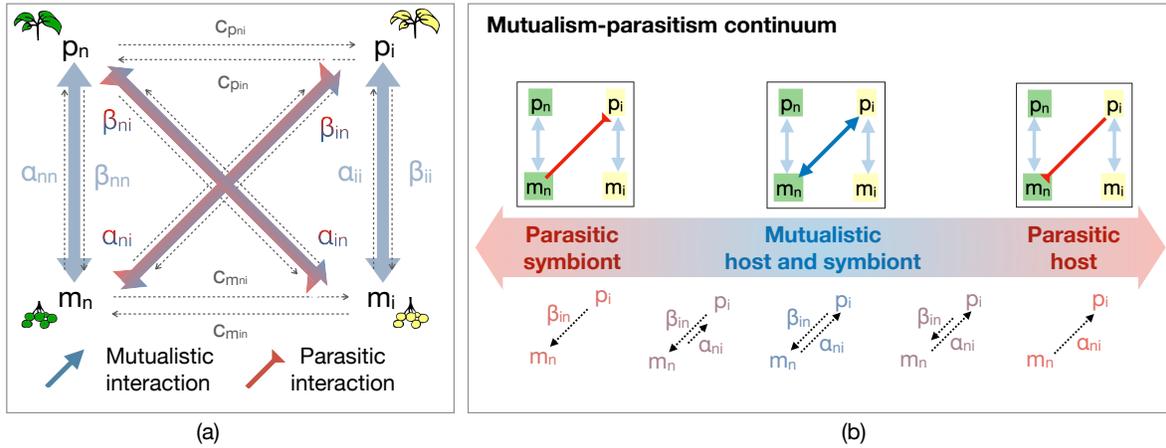


Fig. 1: Schematic representation of the model of Eq. (1). A native microbial community m_n is associated with a host population p_n . Resource exchange between hosts and symbionts is quantified by parameters α_{nn} (symbionts to hosts) and β_{nn} (hosts to symbionts). Similarly, a population of invasive 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 $c_{m_{ni}}$).

137 In addition to resource exchange parameters, resource supply also depends on host and
 138 symbiont densities, as determined by functions F_{p_n} , F_{p_i} , F_{m_n} and F_{m_i} , described in Eqs. (2a-
 139 d). Functions F_{p_n} and F_{p_i} (Eqs. (2a,c)) tell us that when microbial biomass is much smaller
 140 than the total host biomass, the amount of resource that hosts can supply to each symbiont
 141 is limited by microbial biomass (i.e., by what symbiont can take), adjusted by the factor
 142 $1/d$. Thus, each host species will supply to its symbionts an amount of resource proportional
 143 to symbiont biomass, and to the relative abundance of the host species in the whole host
 144 population, where the presence of other symbionts in the community may reduce this amount.

145 When host biomass is much smaller than the total symbiont biomass (adjusted by the
 146 factor $1/d$) the amount of resource that a host can supply to its symbionts is limited by host
 147 biomass (e.g., by what the host can give). Each symbiont will supply to its host an amount
 148 of resource proportional to host biomass, and to the proportion of biomass occupied by the
 149 symbiont in the whole symbiont community. The presence of additional hosts may also reduce
 150 this amount. Analogously, functions F_{m_n} and F_{m_i} (Eqs. (2b,d)) tell us that the amount of
 151 resource that symbionts supply to hosts is limited by symbiont biomass, when host biomass is

152 large compared to the total symbiont biomass, and by symbiont biomass, when host biomass
 153 is smaller than the total symbiont biomass (adjusted by the factor d).

154 2.2 Model analysis and scenarios of interest

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

160 Specifically, we consider the model of Eq. 1 in the case of a host population p (either p_n
 161 or p_i) interacting with its microbial community m (either m_n or m_i). We obtain:

$$162 \begin{cases} \frac{dp}{dt} = r_p p + \frac{pm}{\frac{p}{d} + m} \underbrace{\left(q_{hp} \frac{\alpha}{d} - q_{cp} \beta \right)}_{:=Q_p} - \mu_p p^2, \\ \frac{dm}{dt} = \frac{pm}{\frac{p}{d} + m} \underbrace{\left(q_{cm} \beta - q_{hm} \frac{\alpha}{d} \right)}_{:=Q_m} - \mu_m m^2. \end{cases} \quad (3)$$

163 The association between p and m is mutualistic for $Q_p, Q_m > 0$, parasitic for the host popula-
 164 tion if $Q_p < 0$ and $Q_m > 0$, and parasitic for the microbial community if $Q_p > 0$ and $Q_m < 0$.
 165 Note that the values of Q_p and Q_m depend on parameters α and β , which characterise the
 166 quality of the resource exchange between p and m .

167 We restrict our attention to the case where the association between native hosts and
 168 native symbionts (i.e., between m_n and p_n) and between invasive hosts and invasive symbionts
 169 (i.e., between m_i and p_i) is mutualistic. We then consider the possible outcomes when the
 170 associations between native symbionts m_n and invasive hosts p_i (Fig. 2, left) and between
 171 invasive symbionts m_i and native hosts p_n (Fig. 2, right) can be mutualistic or parasitic.

172 For instance, the association between a native host p_n and invasive microbial symbionts
 173 m_i is mutualistic as long as

$$174 Q_p > 0 \iff \alpha_{in} > \frac{q_{cp_n} \beta_{ni} d}{q_{hp_n}} \quad \& \quad Q_m > 0 \iff \beta_{ni} > \frac{q_{hm_i} \alpha_{in}}{q_{cm_i} d}, \quad (4)$$

175 and parasitic for either the host or the symbiont if $Q_p < 0$ or $Q_m < 0$. Analogously, association
 176 between invasive hosts p_i and native microbial symbionts m_n is mutualistic for both hosts and
 177 symbionts if

$$178 \alpha_{ni} > \frac{q_{cp_i} \beta_{in} d}{q_{hp_i}} \quad \& \quad \beta_{in} > \frac{q_{hm_n} \alpha_{ni}}{q_{cm_n} d}, \quad (5)$$

179 (see also SI B.2 for more details).

180 The straight lines defined by Eqs. (4) and (5), in the α, β parameter space, mark the
 181 borders between the different regions (parasitic symbiont, mutualistic symbiont and host, and
 182 parasitic host) in Fig. 2, in which interactions between an invasive host population p_i and a
 183 native symbiont community m_n is considered (left plot), or interactions between a native host
 184 population p_n and an invasive symbiont community m_i is considered (right plot). Equality
 185 in either terms of Eqs. (4) and (5) represents cases in which either hosts or symbionts are
 186 commensals.

187 We obtain seven different scenarios, which are identified in Fig. 2: ① Invasive and native
 188 hosts do not share symbionts; a mutualistic association is observed between ② invasive hosts
 189 and a native symbionts, or ③ native hosts and invasive symbionts; a parasitic association

190 is observed, in which native/invasive symbionts exploit invasive/native hosts ((4) and (6)),
 191 or invasive/native hosts exploit native/invasive symbionts ((5) and (7)). The mathematical
 192 analysis of these scenarios and their biological significance will be discussed in section 3.2.
 193 Combinations of these scenarios will also be considered in section 3.3.

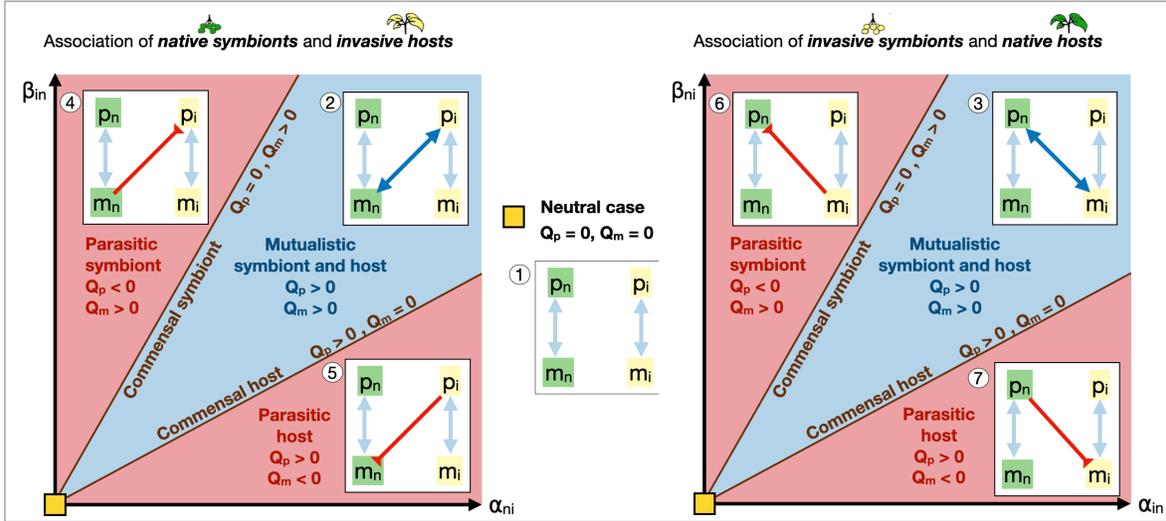


Fig. 2: Novel host-symbiont interactions between native microbes and invasive hosts (left plot) or between native hosts and invasive microbes (right plot) can be parasitic or mutualistic, depending on the value of parameters α_{in} , α_{ni} , β_{ni} and β_{in} , quantifying the resource exchange capacity 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 Eq. (3) and Eqs. (4) and (5).

194 3 Results

195 3.1 Overview of model analysis

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

202 A detailed mathematical analysis of these scenarios is presented in the SI B-E, which
 203 include: the analysis of the one host - one symbiont system, which is crucial to define the
 204 parasitic/mutualistic interactions between a host population and its symbionts community
 205 (section B); the analysis of the one host - two symbiont system (section C), which is important
 206 to understand the dynamics of a host population (native or invasive) associating with both
 207 native and invasive symbionts; the analysis of the one symbiont - two hosts system (section D),
 208 providing insights on the dynamics of a symbiont community (native or invasive) associating
 209 with native and invasive hosts; and the analysis of the two hosts - two symbionts system
 210 exposed according to the scenarios described in (1)-(7) (section E). We refer to invasion as a
 211 situation in which the successful establishment and persistence of invasive hosts, symbionts
 212 or both is possible. Exploration of alternative scenarios not presented in this paper, such
 213 as specific scenarios corresponding to different parameter combinations, can be conducted

214 through numerical simulations of Eq. (1). For precisely this purpose, a user-friendly version
215 of the code is made publicly available on the modelRxiv platform (Harris et al., 2022) (<https://modelrxiv.org/model/YfndNX>).
216

217 3.2 Scenarios of interest

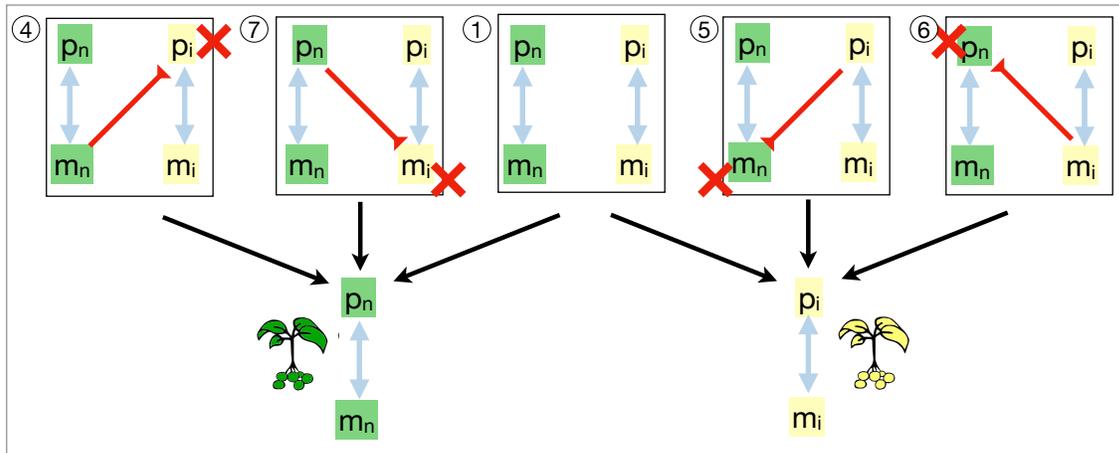
218 **① Native and invasive species do not share symbionts nor hosts.** When neither
219 symbionts nor hosts are shared between native and invasive species, and competition within
220 hosts and between symbionts is strong, competitive exclusion of one host-symbiont commu-
221 nity, either the native or the invasive one, occurs through selection due to trait differences
222 (represented in the model through differences in model parameters α , β , q , c , μ , or r_p , which
223 can be explored numerically), or through differences in initial abundance. When selection due
224 to trait differences occurs, the host-symbiont association that provides the highest fitness to
225 either hosts or symbionts outcompetes the other. Note that in this case, more mutualistic
226 associations are expected to provide highest fitness, and therefore provide resilience against
227 invasion. Differences in initial abundance can also favor one host-symbiont community over
228 the other (see also Fig. E.1①). Indeed, differences in the initial abundance of symbionts (or
229 hosts) affect host (or symbiont) growth rate and, in turn, symbiont (or host) growth rate,
230 providing a competitive advantage to the community with the largest abundance of hosts or
231 symbionts.

232 **② The association between native symbionts and invasive hosts is mutualistic**

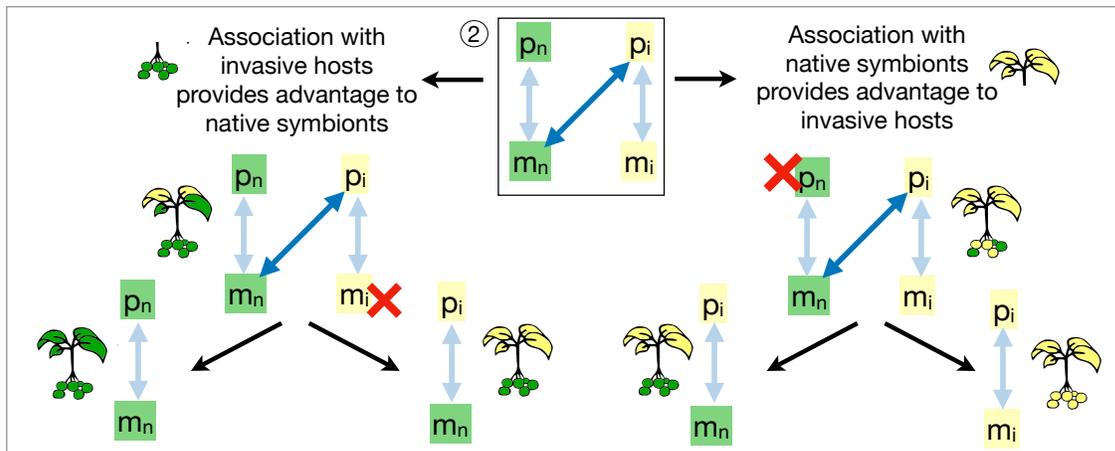
233 • *Association with native symbionts provides advantage to invasive hosts:* Association
234 with native symbionts can increase the fitness of invasive hosts, and provide them with
235 a competitive advantage that can lead to competitive exclusion of native hosts (Fig. 3b,
236 right pathways, and SI E and Fig. E.1② for mathematical insights). Subsequently, inva-
237 sive symbionts may outcompete native symbionts, e.g., if native symbionts are weakened
238 by the absence of native hosts or if invasive symbionts are empowered by an increase
239 in invasive hosts (Fig. 3a, far right pathway, leading to association between p_i and m_i).
240 Alternatively, invasive symbionts may be outcompeted by native symbionts (Fig. 3a,
241 centre right pathway, leading to association between p_i and m_n).

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

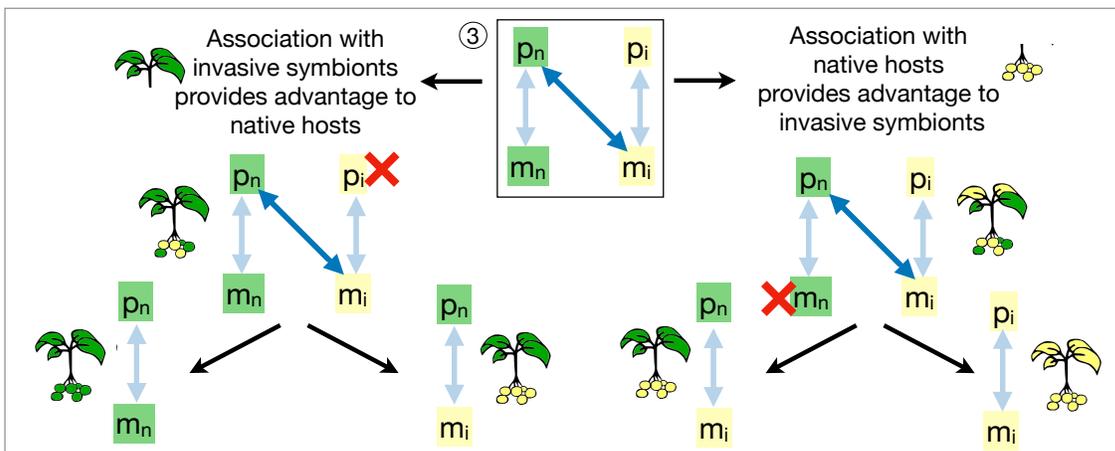
252 Note that when considering the case in which native and invasive species do not share
253 symbionts (i.e., scenario ①) less mutualistic host-symbiont associations are expected to
254 have lower fitness with respect to more mutualistic host-symbiont associations, and are
255 thus not likely to invade.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



(a)



(b)



(c)

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.

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

272 ③ The association between native hosts and invasive symbionts is mutualistic

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

282 A variation of the latter scenario is the situation in which invasive symbionts are not
 283 completely harmful to native hosts, but are low quality mutualists. In this case, the sub-
 284 stitution of native symbionts with invasive symbionts may lead to a loss in the biomass
 285 of native hosts (Fig. 4b). Invasive microbes may then continue to be present in the
 286 environment and negatively affect ecosystem functionality long after the disappearance
 287 of their invasive hosts.

288 • *Association with invasive symbionts provides advantage to native hosts:* Association
 289 with invasive symbionts can also provide an advantage to native hosts, which then
 290 outcompete invasive hosts (Fig. 3c, left pathway and Fig. E.1(3)). If invasive symbionts
 291 are strong competitors, they may subsequently exclude native symbionts, which would
 292 lead to the formation of novel associations between invasive symbionts and native hosts,
 293 and to microbial invasion (Fig. 3c center left pathway, leading to association between
 294 p_n and m_i). This scenario may be more likely to occur, as it can be observed through
 295 two different pathways. No invasion occurs if invasive symbionts suffer from the absence
 296 of invasive hosts and are outcompeted by native symbionts (Fig. 3b far left pathway,
 297 leading to associations between p_n and m_n).

298 ④ **Native symbionts are parasitic to invasive hosts.** The association of native symbionts
 299 with invasive hosts can provide biotic resistance to native host-symbiont associations (Fig. 3a,
 300 pathway ④ and SI E and Fig. E.1(4)). This can occur, for example, if parasites that are only
 301 slightly harmful to native hosts, e.g., because they have co-evolved with them, cause a strong
 302 reduction in the fitness, or death, of invasive hosts. The death of invasive hosts would then
 303 be followed by the death of their symbionts. Poor adaptation of invasive species to native
 304 symbionts can also lead to exploitation of invasive hosts by native symbionts. This can occur,

305 for example, if native symbionts weaken invasive hosts by receiving a certain resource at low
306 cost (see also Fig. D.2 for details).

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

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

327 **⑦ Native hosts are parasitic to invasive symbionts.** Interaction of native hosts with
328 invasive symbionts can provide resilience against invasion, if native hosts are harmful to in-
329vasive symbionts (Fig. 3a, pathway ⑦ and SI E and Fig. E.1⑦). Here, we consider that a
330 native host can take advantage of invasive symbiont to the symbiont’s detriment, preventing
331 the establishment of invasive symbionts and their hosts (see also Fig. C.1).

332 **3.3 Combined scenarios**

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

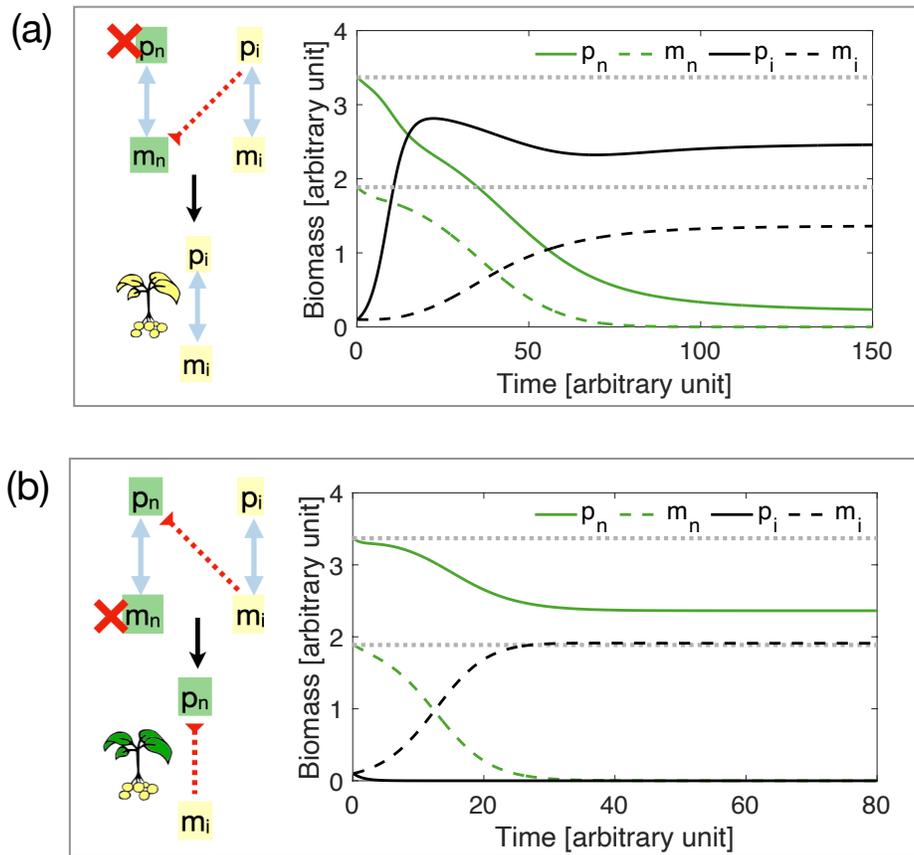


Fig. 4: (a) Possible dynamics of co-invasion occurring when invasive hosts are low quality mutualists, and exploit native symbionts at the indirect expense of native hosts. In this case, the resulting community will have lower biomass with respect to the displaced invasive community (compare black curves 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>).

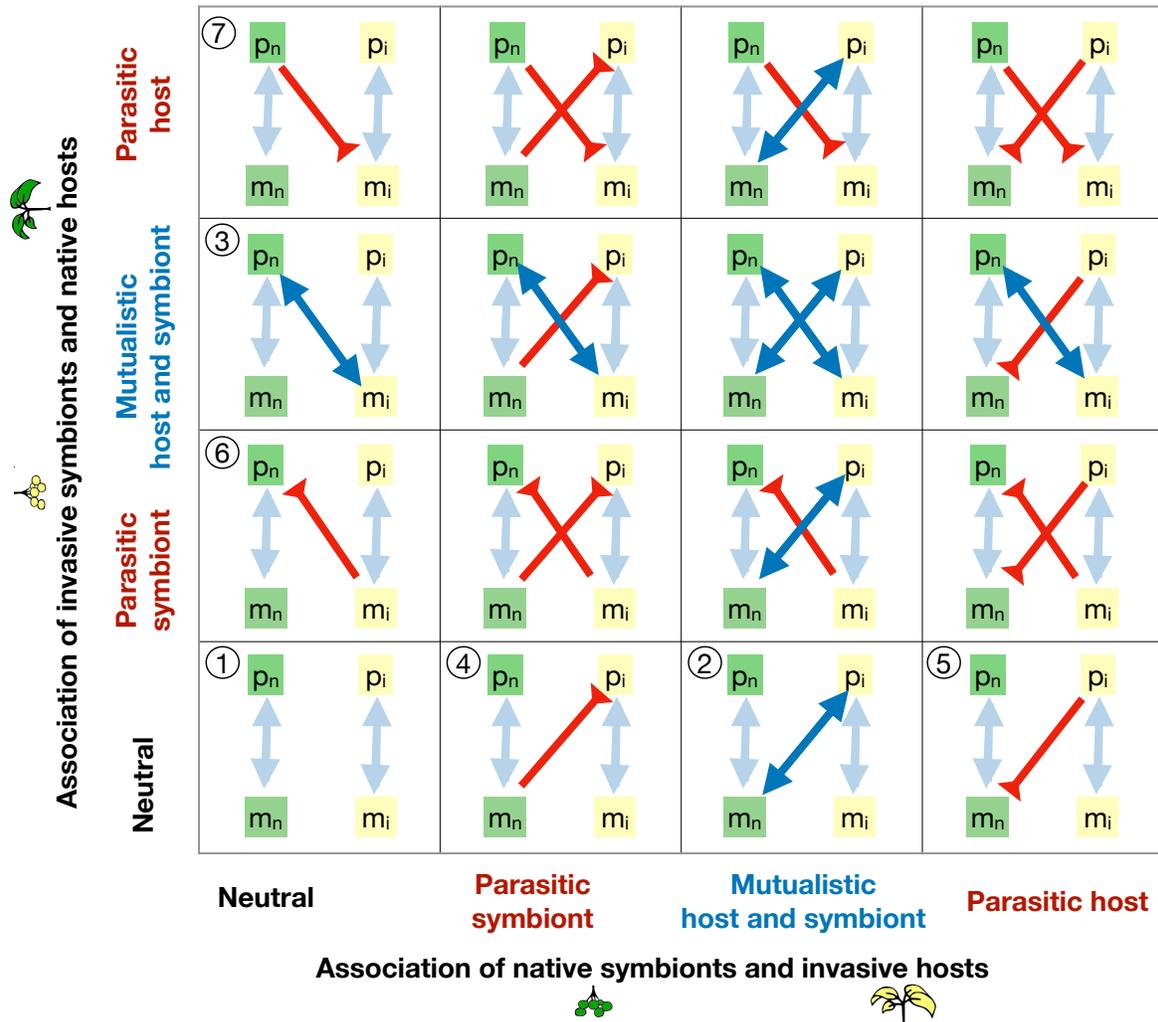


Fig. 5: Schematic representation of possible interaction scenarios that can be explored within our framework. The seven numbered circles indicate the seven scenarios discussed in the results section. Other scenarios can be understood as combination of these seven. Interactive simulation of these and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

346 4 Discussion

347 It has been known for some time that the formation of novel host-symbiont associations can
 348 facilitate invasion, as well as provide resilience to native communities (Bever et al., 2010;
 349 Dickie et al., 2017). We show here that these general observation can be dissected into
 350 several different mechanisms, which we use to create a global framework for broadening our
 351 understanding of invasion dynamics.

352 4.1 Host-symbiont interactions increase invasion risk

353 A growing number of empirical studies, particularly on plant-fungal associations, have shown
 354 that invasion can occur when invasive hosts form novel mutualistic associations with native
 355 symbionts, eventually increasing host competitive ability (Callaway et al., 2004; Ted-
 356 ersoo et al., 2007; Moeller et al., 2015; Shipunov et al., 2008). Strong evidence also shows

357 that pathogens co-introduced with invasive hosts may weaken native host populations, which
358 favours their competitive exclusion by invading hosts in a dynamic often referred to as ‘disease-
359 mediated invasion’ (Anderson et al., 2004; Parker and Gilbert, 2004; Desprez-Loustau et al.,
360 2007; Santini et al., 2013; Carnegie et al., 2016). We highlight the possibility that some of
361 these mechanisms may occur not only when shared symbionts are either pathogens or mu-
362 tualists, but also when the mutualistic quality of introduced symbionts differs from that of
363 native symbionts. For instance, introduced symbionts that are slightly less mutualistic than
364 those found in native communities might lead to a decrease in biomass of native hosts
365 (Bever, 2002) (e.g., see our Fig. 4b). Similarly, the acquisition of native symbionts that are
366 slightly more mutualistic than the original invasive community can help a host to invade (see
367 Fig. 4a). These changes in population growth and abundance may not be sufficient to directly
368 drive a community to extinction (as for the acquisition of pathogenic microbes), but they may
369 be enough to provide a competitive advantage to a population with respect to another and
370 change the invasion dynamics (Levine et al., 2004).

371 In addition to highlighting the possible dynamics along the mutualism-parasitism contin-
372 uum, we would like to emphasize the importance of considering invasion dynamics arising at
373 the community level, that accounts for host-symbiont interactions, as well as host-host and
374 symbiont-symbiont interactions. Considering only host-symbiont interactions may lead to the
375 misconception that only the host-symbiont community that provides the highest fitness to
376 their hosts and symbionts may co-invade and displace native host-symbiont communities, as
377 observed in some instances (Dickie et al., 2010; Nunez and Dickie, 2014; Hayward et al., 2015).
378 However, when accounting for the possibility that symbiont disruption and exchange among
379 native and invasive species may occur (Dickie et al., 2017; Catford et al., 2009; Mitchell et al.,
380 2006), co-invasion of a less fit host-symbiont community may be observed (Fig. 4a). Thus, un-
381 derstanding the whole range of possible outcomes following the introduction of a new species
382 requires to embrace a community perspective that accounts for interactions among multiple
383 hosts and symbionts (Dickie et al., 2017; Fahey and Flory, 2022).

384 In some instances, the formation of novel host-symbiont interactions may lead to changes
385 in total community biomass with long-term repercussions on ecosystem functionality (Nunez
386 and Dickie, 2014; Lovett et al., 2006; Dickie et al., 2011; Mitchell and Power, 2003; Cobb and
387 Rizzo, 2016; Preston et al., 2016; Ehrenfeld, 2010). Although this reduction in community
388 biomass is well-known for pathogen spread (Lovett et al., 2006; Mitchell and Power, 2003; Cobb
389 and Rizzo, 2016; Preston et al., 2016), here we present alternative mechanisms that can lead
390 to an invasion-driven biomass decrease through higher-order interactions (Billick and Case,
391 1994; Mayfield and Stouffer, 2017). For example, if invasive hosts provide a reduced reward as
392 compared to natives (Hoffman and Mitchell, 1986; Mummey and Rillig, 2006; Hausmann and
393 Hawkes, 2009; Vogelsang and Bever, 2009), associations between invasive hosts and native
394 symbionts will lead to the direct exploitation of the resources provided by native symbionts.
395 In addition, there will be indirect exploitation of more mutualistic native hosts that invested
396 resources in the growth of a large native microbial community from which it can no longer
397 fully benefit. Thus, in this case, an increase in the abundance of invasive hosts, facilitated by
398 the presence of native host-symbiont communities, occurs in conjunction with a decrease in
399 the abundance of native symbionts and their hosts (e.g., see Fig. 4a).

400 4.2 Host-symbiont interactions increase community resilience

401 Less studied than the role of host-symbiont associations in invasion dynamics is their role in
402 providing resilience to native communities (Van der Putten et al., 2010; Zenni and Nuñez,
403 2013; Levine et al., 2004). In spite of its importance to community assembly (Wu et al.,
404 2024), invasion failure remains poorly understood in practice Diez et al. (2009); Zenni and

405 Nuñez (2013). Given that novel host-symbiont associations may be the key to understand
406 invasion success, they may also underlie mechanisms providing resistance to invasion. Indeed,
407 mechanisms of symbiont disruption and replacement, as well as differences in community
408 composition and emerging properties following species introduction, may lead to changes in
409 resource exchange dynamics between hosts and symbionts and, possibly, provide resistance to
410 invasion (Levine et al., 2004; Dinoor and Eshed, 1984; Beckstead and Parker, 2003; Knevel
411 et al., 2004).

412 A clear example of host-symbiont associations driving invasion failure is the transmission
413 of native pathogens to invasive plants (Hood et al., 2008; Piou et al., 2002). This novel
414 association can provide biotic resistance against invaders (Mordecai, 2013; Flory and Clay,
415 2013; Prev y and Seastedt, 2015). Other, more complex, dynamics of biotic resistance occur
416 when native symbionts, which have co-evolved with native hosts, are highly mutualistic to
417 native hosts but not to invasive hosts (Bunn et al., 2015; Moora et al., 2011). Here we show
418 that association with these low-quality mutualistic symbionts can harm invasive hosts, and
419 allow for their competitive exclusion by native hosts (as described in  2) and  4).

420 Finally, less competitive host-symbiont pairs may resist invasion by associating with mu-
421 tualistic invasive symbionts (Mordecai, 2013; Flory and Clay, 2013). Reports of spread of
422 invasive symbionts in native habitats are numerous (Dickie et al., 2016; Wolfe and Pringle,
423 2012; Berch et al., 2017; Mallon et al., 2015; Hart et al., 2017; Golan et al., 2024). However,
424 the ecological consequences of these new associations are unclear. Our framework can guide
425 new empirical research to understand under which circumstances these associations can pro-
426 vide natives with biotic resistance to host invasion, and when they may instead lead to a risk
427 of facilitating symbiont invasion.

428 4.3 Framework limitations and possible extensions

429 Our framework allows for the mechanistic exploration of the interactions between microbes and
430 their hosts, and can produce a rich variety of theoretical scenarios. Parameterization based
431 on realistic biological scenarios that consider the specificity of host-symbiont interactions and
432 variability in their contribution to fitness can provide insights into possible invasion dynamics
433 through numerical simulations (e.g., through the tool we provide on the modelRxiv platform
434 Harris et al. (2022)). These simulations, can help us determine which scenarios are more likely
435 to be observed in particular settings.

436 The framework presented here also provides a strong basis for new mathematical investi-
437 gation. Our model accounts for multiple levels of interactions -such as interactions between
438 hosts, between symbionts, and between hosts and symbionts-, it considers biologically plausible
439 density-dependent functional responses (as shown in Eqs. (2)), as well as an asymmetry in their
440 dependence on the mutualism (i.e., obligate or facultative). Thus, the effect of higher-order
441 interactions in our system may differ from what observed in previous studies that considered
442 only microbial or only host communities, and that used linear, instead of density-dependent,
443 functional responses (e.g., Gibbs et al. (2022)). Additionally, an extension of this framework
444 to account for associations between multiple hosts and symbionts (e.g., to consider a microbial
445 community composed of multiple microbial strains in which invasive hosts preferentially sup-
446 port certain microbial strains over others (Callaway et al., 2001; Bever, 2002; Kohout et al.,
447 2011)), could help us investigate the effect of higher-order interactions on coexistence and di-
448 versity of large host-symbiont communities. Such an extension to our framework is presented
449 in SI F) Other possible extensions include the evolution of host-symbiont associations, such
450 as the evolution of host adaptation to pathogens (Thrall et al., 2002), or 'parasite-spillback'
451 mechanisms (Flory and Clay, 2013; Strauss et al., 2012; Kelly et al., 2009; Mangla et al.,
452 2008; Day et al., 2016), where invasive hosts associate with native pathogens that increase in

453 abundance on invasive hosts, leading to increased colonization of native hosts.

454 **5 Conclusion**

455 Multi-species interactions involving native and invasive hosts and their symbionts can play
456 an important role in invasion dynamics, and our ability to accurately evaluate invasion risks
457 has been shown to depend their intricate dynamics. While classical theory has mostly focus
458 on the individual invasion of either host species or their microbial symbionts, consideration
459 on the possible formation of novel host-symbiont associations between native and non-native
460 symbionts and their native and non-native hosts can shed light on new modalities of invasion
461 that have not been considered so far. Thus, less mutualistic hosts and symbionts can in-
462 vade through exploitation of pre-existing symbiotic relationships, or introduced microbes can
463 increase their invasiveness through association with native hosts. We present a mechanistic
464 mathematical framework that explicitly accounts for host-symbiont mutualistic and parasitic
465 associations, to deepen our understanding of invasion biology in ecological communities and
466 guide empirical research.

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734 **Supplementary information**

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774 **A Numerical simulations**775 **A.1 Overview of interaction scenarios and default parameter values**

776 A brief description of model parameters and their default values used for the simulations is
 777 provided in Table A.1. The value of the resource exchange parameters α and β for each of
 778 the 7 scenarios described in Fig. 2 are provided in Table A.2. Specific parameters used for
 779 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.

780 A.2 Scenarios on ModelRxiv

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

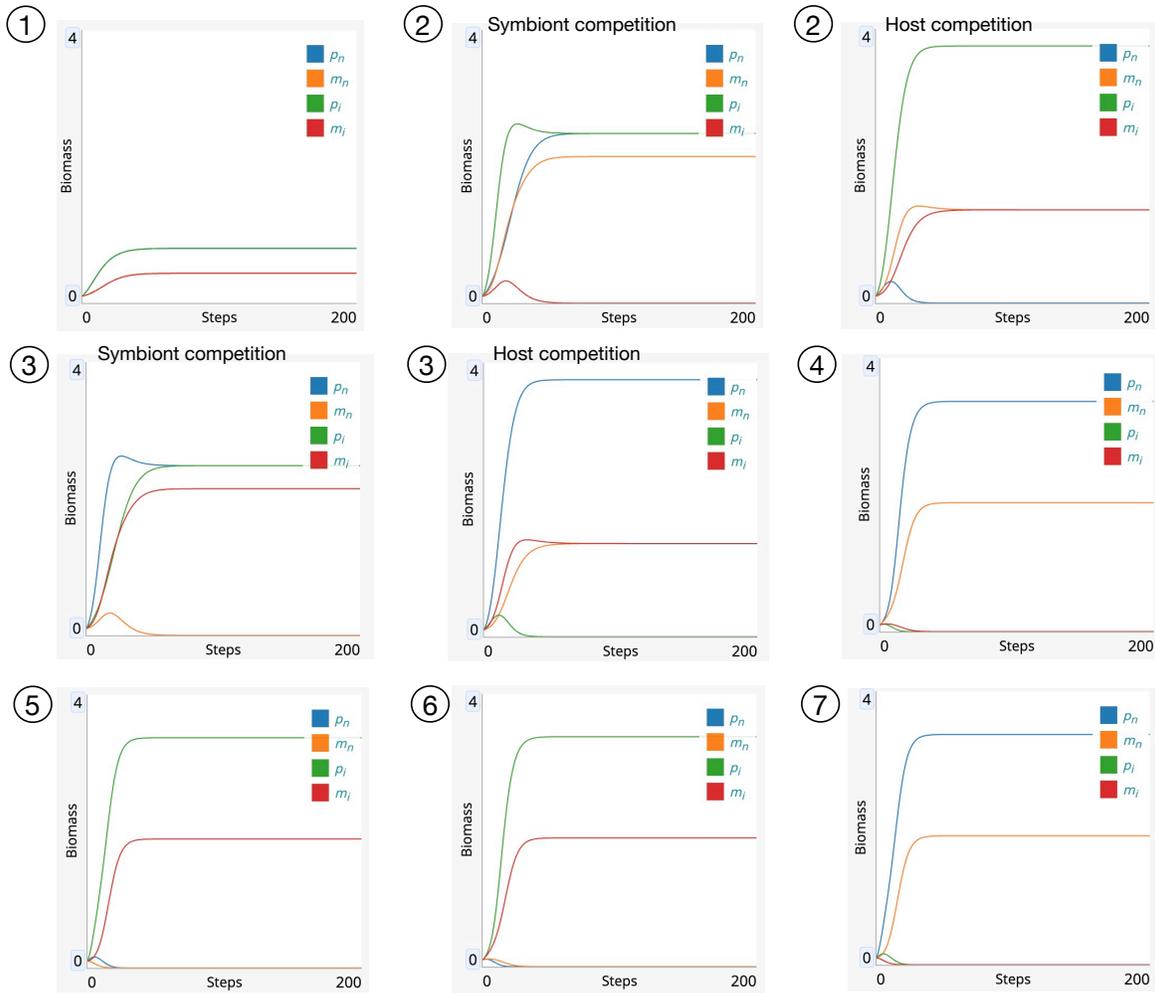


Fig. A.1: Timeseries produced by scenarios 1-7 described in Fig. 2, for the parameter combinations provided in Table A.2 and Table A.2. Note that in scenarios 2 and 3 coexistence of hosts or symbionts is unstable when competition is strong, and differences in model parameters or in initial conditions 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. (3):

$$\begin{cases} \frac{dp}{dt} = r_p p + \frac{pm}{\frac{p}{d} + m} Q_p(\alpha, \beta) - \mu_p p^2, \\ \frac{dm}{dt} = \frac{pm}{\frac{p}{d} + m} Q_m(\alpha, \beta) - \mu_m m^2, \end{cases} \quad \text{where} \quad \begin{cases} Q_p(\alpha, \beta) = q_{hp} \frac{\alpha}{d} - q_{cp} \beta, \\ Q_m(\alpha, \beta) = q_{cm} \beta - q_{hm} \frac{\alpha}{d}. \end{cases} \quad (6)$$

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. (6) 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

$$p^* = p_0 + \frac{\frac{Q_p Q_m}{\mu_m \mu_p}}{\frac{S}{d} + \frac{Q_m}{\mu_m}}, \quad \text{and} \quad m^* = \frac{d Q_m}{\mu_m} \frac{\frac{S}{d}}{\frac{S}{d} + \frac{Q_m}{\mu_m}} \quad (7)$$

where S is the total biomass, $S = p^*/d + m^*$ and it satisfies

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

The phase plane of the system of Eq. 6, 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*, and 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

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

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

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

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

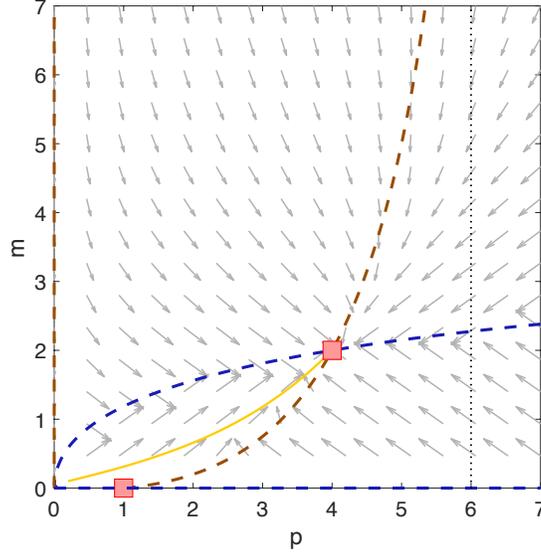


Fig. B.1: (a) Phase plane corresponding to the system of equations (6), for which $r_p > 0$. Brown dashed lines are nullclines found for $dp/dt = 0$, while blue dashed lines are nullclines found for $dm/dt = 0$. Intersection of the two non-zero nullclines corresponds to the stable steady state (p^*, 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 $p = Q_p/\mu_p$.

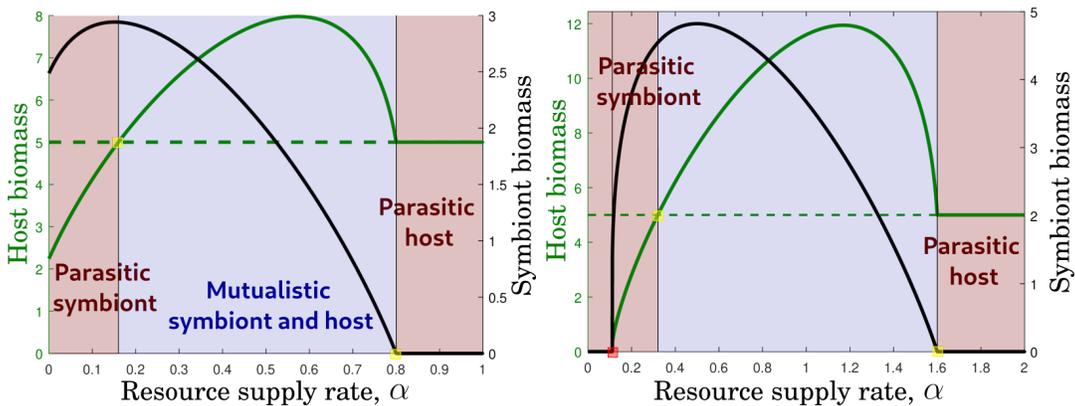


Fig. B.2: Host (green plain curve) and symbiont (black plain curve) biomass at equilibrium (p^*, m^*) defined by (7), with respect to the resource exchange rate α of the symbiont. The host exchange rate β is fixed to $\beta = 0.4$ (left panel) and $\beta = 0.8$ (right panel). The dashed line corresponds 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 $\alpha = \beta dq_{cm}/q_{hm}$. 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 (6). We obtain:

$$J(p^*, m^*) = \frac{1}{\frac{p^*}{d} + m^*} \begin{pmatrix} \frac{m^{*2}}{\frac{p^*}{d} + m^*} Q_p + (r_p - 2\mu_p p^*) \left(\frac{p^*}{d} + m^* \right) & \frac{\frac{p^{*2}}{d}}{\left(\frac{p^*}{d} + m^* \right)} Q_p \\ \frac{m^{*2}}{\left(\frac{p^*}{d} + m^* \right)} Q_m & \frac{\frac{p^{*2}}{d}}{\frac{p^*}{d} + m^*} Q_m - 2\mu_m m^* \left(\frac{p^*}{d} + m^* \right) \end{pmatrix}. \quad (8)$$

From Eq. (6), 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

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

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

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

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 $\text{Det} J > 0$. We have

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

The positivity of the determinant follows from the following inequality

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

814 Therefore, we showed that when the unique positive stable steady state (p^*, m^*) exists, that
 815 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
 816 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

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

817 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:

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

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

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

818 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

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

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

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

819 By combining the two systems, we obtain

$$820 \quad \frac{\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{Q}_p}{\mu_p} \mathbf{m} = S^2 \mathbf{m} - S \mathbf{C}_m^{-1} \mathbf{Q}_m p_0 \quad \text{and} \quad \frac{\mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m}{\mu_p} p = S^2 (p - p_0).$$

We can reformulate the system as follows:

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

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

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

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

We can compute \mathbf{m} as follow

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

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

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

where $\mathbf{e} = (1, \dots, 1)$. 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

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

822 Finally, we get

$$823 \quad p = p_0 + \frac{\frac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}}{\frac{S}{d} + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c}} \quad \text{and} \quad \mathbf{m} = \frac{S}{\frac{S}{d} + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c}} \mathbf{C}_m^{-1}\mathbf{Q}_m. \quad (9)$$

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:

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

The two last inequalities imposes that

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

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

827 C.2 Parasitic versus mutualistic behaviour of host and symbiont

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

831 **Parasitic host.** A host associated with a native mutualistic symbiont can be parasitic to
832 an invasive symbiont, that competes with the native symbiont ($Q_{m_i} < \mu_m Q_m/c$). The host
833 can be parasitic to the invasive symbiont even if it would have been mutualistic to it in
834 absence of the native symbiont ($Q_{m_i} > 0$). This detrimental effect of the host associated
835 with a native symbiont is due to competition between the two symbionts (see rightmost
836 yellow square in Fig. C.1(b) that shows the transition between mutualistic and parasitic
837 host). Thus the association with a mutualistic symbiont can enhance the parasitic nature of
838 the host with respect to invasive symbionts (compare dashed curve $Q_{m_i} = 0$ with plain curve
839 $Q_{m_i} = \mu_m Q_m/c$ 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

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

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

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

848 The invasive symbiont can be either parasitic or mutualistic to the native host depending
 849 on their exchange rates. For instance in absence of native species, the previous definition of
 850 section B.2 states that if $Q_{p_i} > 0$ the invasive symbiont is *mutualistic* to the host, while if
 851 $Q_{p_i} < 0$ then the symbiont is also *parasitic* to the host. However, this definition only compare
 852 the biomass of the host with and without the invasive symbiont. In presence of initial native
 853 symbiont, we may also compare with the host biomass when associated with the mutualistic
 854 native symbiont. We discuss the parasitic/mutualistic nature of the invasive symbiont with
 855 respect to the native host in the following paragraph.

856 **Mutualistic/parasitic invasive symbiont.** In the presence of a native symbiont, the mu-
 857 tualistic nature of the interaction between the native host and the invasive symbiont may
 858 vary when comparing with the scenario without a native symbiont, that competes with the
 859 invasive symbiont. In both situations, the invasive symbiont is *mutualistic* to the host, if the
 860 biomass of the native host is larger than the biomass of the native host when alone with or
 861 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

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

862 The transition between a mutualistic and parasitic invasive symbiont is illustrated by the
 863 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

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

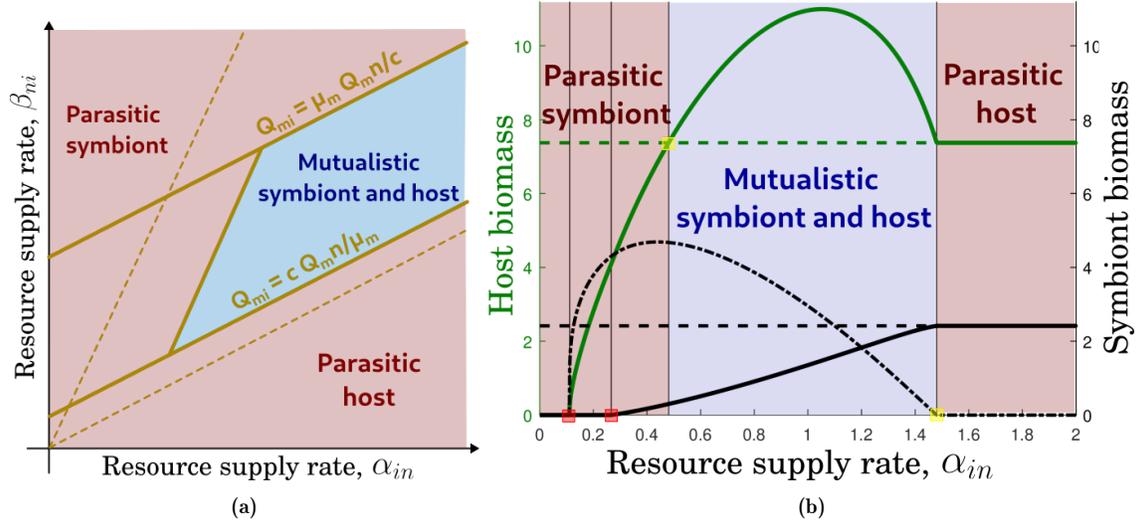


Fig. C.1: Parasitic or mutualistic invasive symbiont and native host. Evolution of the host (green plain curve) and symbiont (black plain curve) biomass at equilibrium defined by (9), with respect to the exchange rate α_{in} of the invasive symbiont to the native host. The exchange rates between native 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).

864

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:

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

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

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

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

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

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 ;

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

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

$$c_p \leq \mu_p.$$

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

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

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

868 Combining the two systems, we obtain:

$$869 \quad \frac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m} m = S^2 m - S \frac{\mathbf{Q}_m}{\mu_m} \mathbf{p}_0 \quad \text{and} \quad \frac{\mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{Q}_m}{\mu_m} \mathbf{p} = S^2 (\mathbf{p} - \mathbf{p}_0).$$

We can reformulate the system as follows:

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

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

Observing that $\text{Tr}(\mathbf{A}) = \frac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m}$ and $\mathbf{A}^k = \left(\frac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m} \right)^{k-1} \mathbf{A}$ 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

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

871 D.2 Parasitic versus mutualistic behaviour of host and symbiont

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

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

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

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

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

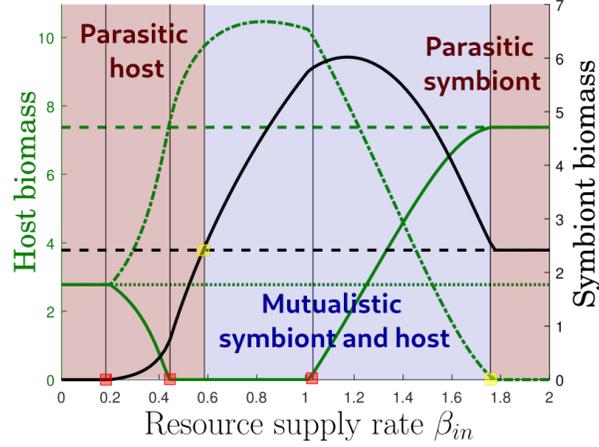


Fig. D.2: Parasitic or mutualistic invasive host and native symbiont. Evolution of the native host (solid green curve), invasive host (dashed green curve) and symbiont (solid black curve) biomass at equilibrium defined by (9), with respect to the exchange rate β_{in} of the invasive host to the native 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).

888

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

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

and

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

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

$$\begin{cases} \frac{dp_n}{dt} = r_{p_n}p_n + \frac{p_n}{\frac{p_n}{d} + \frac{p_i}{d} + m_n + m_i} (m_n Q_p + m_i Q_{p_{ni}}) - \mu_p p_n^2 - c_p p_i p_n, \\ \frac{dm_n}{dt} = \frac{m_n}{\frac{p_n}{d} + \frac{p_i}{d} + m_n + m_i} (p_n Q_m + p_i Q_{m_{in}}) - \mu_m m_n^2 - c_m m_i m_n, \\ \frac{dp_i}{dt} = r_{p_i}p_i + \frac{p_i}{\frac{p_n}{d} + \frac{p_i}{d} + m_n + m_i} (m_i Q_p + m_n Q_{p_{in}}) - c_p p_n p_i - \mu_p p_i^2, \\ \frac{dm_i}{dt} = \frac{m_i}{\frac{p_n}{d} + \frac{p_i}{d} + m_n + m_i} (p_i Q_m + p_n Q_{m_{ni}}) - c_m m_n m_i - \mu_m m_i^2. \end{cases} \quad (10)$$

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

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

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

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

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

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

Then, using the notation $\mathbf{p} = (p_n, p_i)$, $\mathbf{m} = (m_n, m_i)$, and $\mathbf{r}_p = (r_{p_n}, r_{p_i})$, the system (10) can be reformulated as

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

895 E.1 Steady states of the system

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

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

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

$$\begin{aligned} (p_n^*, m_n^*, 0, 0) & \text{ native pair} \\ (0, 0, p_i^*, m_i^*) & \text{ invasive pair} \\ (p_n^*, 0, 0, m_i^*) & \text{ mixed pair, invasive symbiont with native host} \\ (0, m_n^*, p_i^*, 0) & \text{ mixed pair, invasive host with native symbiont} \end{aligned} \quad (11)$$

902 Due to our choice of parameters (i.e., with α_{nn} , α_{ii} , β_{nn} and β_{ii} large enough, such that the
 903 association between p_n and m_n and p_i and m_i is mutualistic), the steady state with only native
 904 species or only invasive species always exists. However, the mixed steady states composed of
 905 either a native host with an invasive symbiont, or an invasive host with a native symbiont,
 906 exist only when cross-species interactions between p_n and m_i and between p_i and m_n are
 907 mutualistic, as shown in scenarios ②-③ (see section B.1).

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

This case corresponds to the situation in which a novel association between a host and a
 new symbiont of another host is observed, where the host with two symbionts successively
 outcompete the host. There are two possible steady states of this form :

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

909 These equilibria exist if **competition between the symbionts is weak** and the symbionts are
 910 mutualistic to the host (see section C.1).

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

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

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

912 These equilibria exist if **competition between hosts is weak** and the hosts are mutualistic to
 913 the symbionts (see section D.1).

914 **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 is

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

915 This steady state only exists when **competition between symbionts and between hosts is weak**.

916 **E.2 Outcome of the different interaction scenarios**

917 We first investigate the outcome of the 7 scenarios under strong competition between sym-
 918 bionts and between hosts, that is

$$919 \quad c_p > \mu_p \text{ and } c_m > \mu_m. \quad (12)$$

920 Then, we discuss scenarios ② and ③, that correspond to mutualistic host-symbiont inter-
 921 actions under weak competition to show that inclusion steady state or even coexistence can
 922 occur.

923 **E.2.1 Strong competition between hosts and symbionts**

In this situation, only the exclusion equilibrium, defined in (11) 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

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

924 where p^* , m^* stands for the positive biomass of host and symbiont at equilibrium, $J(p^*, m^*)$ is
 925 defined by (8) in section B.3 and B and I are 2×2 matrices, and I describes the interactions
 926 between the excluded host and symbiont and the surviving ones. From the analysis of Section
 927 B.3, we know that the matrix $J(p^*, m^*)$ has two negative eigenvalues. The matrix I is diagonal
 928 with coefficients that depend on the exclusion equilibrium as follows

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

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

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

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

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

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

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

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

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

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

929 Under strong competition (see condition Eq. (12)), we deduce that the matrices I_{nn} and
 930 I_{ii} have negative coefficients, and the **exclusion steady states with either native or invasive**
 931 **species are stable.**

② **The association between native symbionts and invasive hosts is mutualistic.** In this scenario, association between native symbionts and invasive hosts is mutualistic, that is $Q_{pni} = Q_p > 0$ and $Q_{mni} = Q_m > 0$, while there is no association between native hosts and invasive symbionts, that is $Q_{pin} = 0 = Q_{min}$. The exchange matrices \mathbf{Q}_m and \mathbf{Q}_p become

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

932 Under strong competition, we deduce that the matrices I_{nn} , I_{ii} and I_{ni} have negative coeffi-
933 cients, and the **exclusion steady states with either native or invasive species and the mixed**
934 **steady state of invasive hosts and native symbionts are stable.**

③ **The association native hosts and invasive symbionts is mutualistic.** Similarly to previous scenario, the exchange between invasive symbiont and native host are positive, that is $Q_{pin} = Q_p > 0$ and $Q_{min} = Q_m > 0$, while the exchange between invasive host and native symbiont are null, that is $Q_{pni} = 0 = Q_{mni}$. The exchange matrices \mathbf{Q}_m and \mathbf{Q}_p become

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

935 Under strong competition (Eq. (12)), we deduce that matrices I_{nn} , I_{ii} and I_{in} have negative
936 coefficients, and the **exclusion steady states with either native or invasive species and the**
937 **mixed pair with native host and invasive symbiont are stable.**

④ **Native symbionts are parasitic to invasive hosts.** In this scenario, native symbionts are parasitic to invasive hosts, that is $Q_{pin} = q_p^- < 0$ and $Q_{min} = q_m^+ > Q_m > 0$, while there is no association between native host and invasive symbiont, that is $Q_{pni} = 0 = Q_{mni}$. The exchange matrices \mathbf{Q}_m and \mathbf{Q}_p become

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

938 Under strong competition (Eq. (12)), we deduce that the matrices I_{nn} have negative coeffi-
939 cients. The **exclusion equilibrium with native hosts and symbiont is therefore stable.**

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

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

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

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

940 This inequality may be fulfilled if the symbiont is parasitic in the sense of definition of sec-
941 tion B.2 and the invasive host is mutualistic enough to the symbiont. Otherwise, the native
942 symbiont has to be really parasitic. As a result, when the native symbiont is parasitic enough
943 relative to the invasive host, the equilibrium with **invasive species is unstable.**

⑤ **Invasive hosts are parasitic to native symbionts.** In this scenario, invasive hosts are parasitic to native symbionts, that is $Q_{pin} = q_p^+ > Q_p > 0$ and $Q_{min} = q_m^- < 0$, while there is no association between native hosts and invasive symbionts, that is $Q_{pni} = 0 = Q_{mni}$. The exchange matrices \mathbf{Q}_m and \mathbf{Q}_p become

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

965 **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

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

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

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

971 **① Native and invasive species do not share symbionts nor hosts.** In this scenario,
972 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
973 shown in Fig. E.1①. Which steady state is reached, depends on the initial conditions and
974 model parameters, determining the size of the basin of attraction of each steady state. This
975 situation of bistability is also discussed in scenario ① of the result section and illustrated in
976 Fig. 3(a).

977 **② The association between native symbionts and invasive hosts is mutualistic.** Three
978 steady states are possible, following the formation of novel mutualistic associations between
979 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
980 schematic representation of this scenario is provided in Fig. 3(b). Note that the steady state
981 $(0, m_n^*, p_i^*, 0)$ can be reached through different routes, in orange and yellow in Fig. E.1②. A
982 route in which the density of native symbionts is increased at first (in orange) and a route
983 in which the density of invasive hosts is increased at first (in yellow). These two routes
984 corresponds to the center left and center right pathways in Fig. 3(b).

985 **③ The association between native hosts and invasive symbionts is mutualistic.**
986 Three steady states can be observed following the formation of novel associations between
987 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
988 steady state $(0, m_n^*, p_i^*, 0)$ can be reached through different routes, in orange and yellow in
989 Fig. E.1③. A schematic representation of this scenario is provided in Fig. 3(c). The center
990 left and right pathway in this figure correspond on the orange and yellow pathways in the
991 phase plane. A route in which the density of native symbionts is increased at first (in orange)
992 and a route in which the density of invasive hosts is increased at first (in yellow). These two
993 routes corresponds to the center left and center right pathways in Fig. 3(b).

994 **④ Native symbionts are parasitic to invasive hosts, and ⑦ Native hosts are parasitic**
995 **to invasive symbionts.** In these cases, only one steady state $(p_n^*, m_n^*, 0, 0)$ is stable, as the
996 exclusion of invasive species (either hosts or symbionts) leads to the extinction of their invasive
997 partner, as seen in Fig. E.1④ and ⑦ and in Fig. 3(a).

998 **⑤ Invasive hosts are parasitic to native symbionts, and ⑥ Invasive symbionts are**
999 **parasitic to native hosts.** In these cases, the only stable steady state is $(0,0,p_i^*,m_i^*)$, as
1000 shown in Fig. E.1(⑤) and ⑥ and in Fig. 3(a). This is because the exclusion of native hosts or
1001 symbionts, due to exploitation by invasive species, leads as well to the exclusion of the native
1002 mutualistic partner.

1003 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:

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

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 $i \in \{1, \dots, N\}$ and $j \in \{1, \dots, M\}$ by

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

1004 An analysis of this system is beyond the scope of this paper, and will be left to future work.

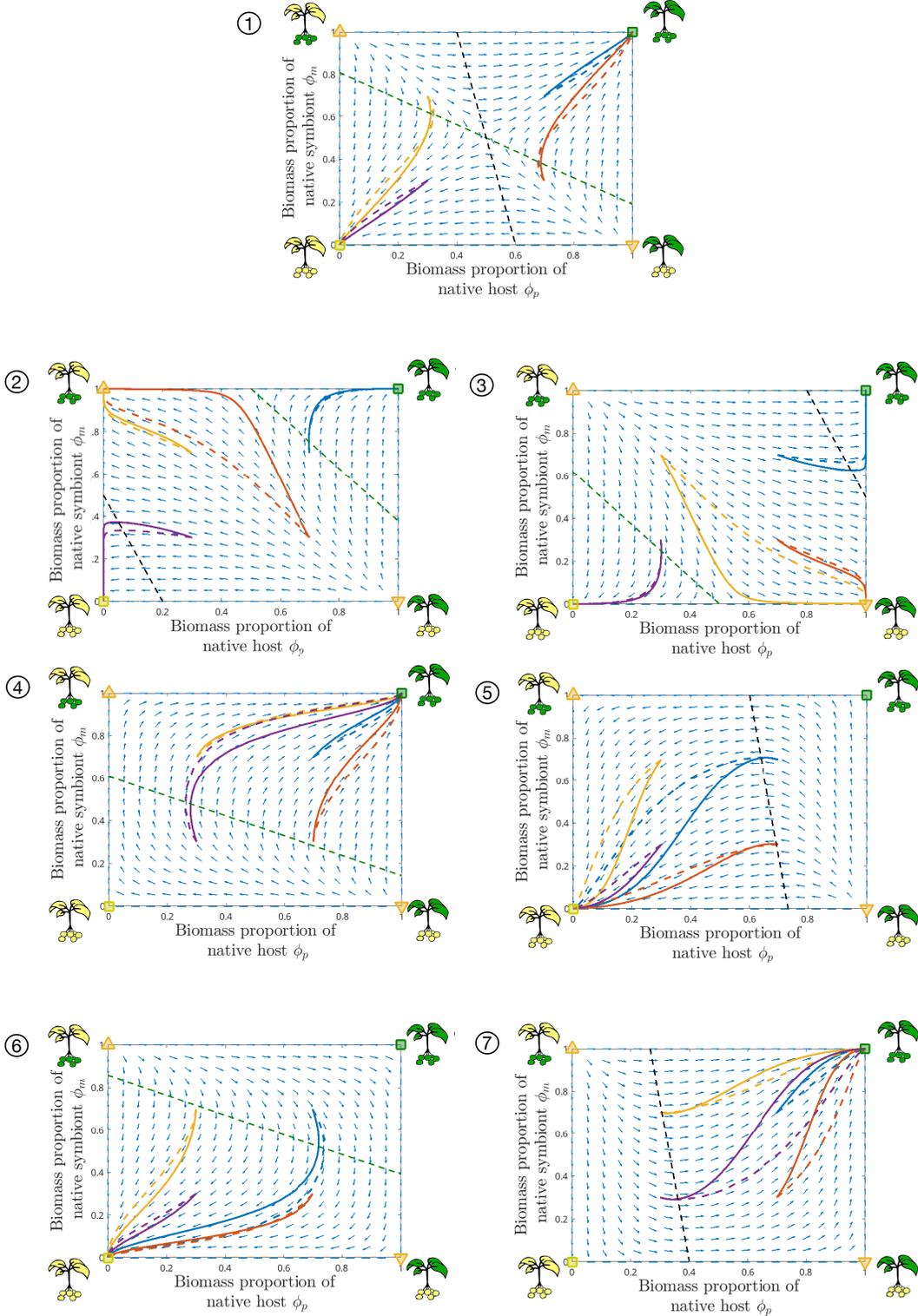


Fig. E.1: Phase plane of the approximation model (13). The green square corresponds to the exclusion equilibrium with native species, the yellow square corresponds to the exclusion equilibrium with invasive species, and the orange triangles correspond to mixed pair equilibria. Shown are 4 trajectories of the full system (10) (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).