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Toward a unified theory of microbially mediated invasion

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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.
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- 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>).

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Author's contributions

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Toward a unified theory of microbially mediated invasion

Abstract

Microbially mediated invasion is an emerging science that aims to account for the role of microbial agents in facilitating or preventing biological invasion. Progress has been made in identifying possible scenarios occurring when microbes can transmit either from native to invasive hosts ('symbiont spillback') or from invasive to native hosts ('symbiont spillover'). For example, the presence of pre-existing mycorrhizal networks in the soil may facilitate plant invasion, and invaders are more likely to be successful if native species are infected with parasites co-introduced with their invasive hosts. However, a unifying theoretical framework to contextualize these individual scenarios and explore the consequences of microbial transmission between hosts along a continuum of beneficial to harmful host-microbial interactions is lacking. Here, we present and analyse such a framework. We discuss interesting scenarios emerging from our analysis and multiple pathways through which microbes can facilitate (or prevent) host invasion, microbial invasion, and the invasion of both hosts and their co-introduced microbes. Our framework provides a new, cohesive and intuition-enhancing perspective on microbially driven dynamics and the way in which the subtleties of the relationships between hosts and microbes affect invasion outcomes.

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

1 Introduction

Biological invasion is often regarded as invasion of single species. Yet, organisms live in symbiosis with a rich and diverse collection of microbes that is an essential component of their host's fitness and reproductive success (Fitzpatrick et al., 2020; Compant et al., 2019; Koskella et al., 2017). Host-associated microbial communities may encompass mutualistic, commensal, and parasitic (or pathogenic) symbionts that may benefit or harm the host to different extents. While the presence of parasitic symbionts may lead to reduced host growth, mutualistic symbionts may increase host fitness and health by carrying out important metabolic and protective functions, such as increasing resource provisioning, or by protecting a host against infection (Smith and Read, 2010; Peixoto et al., 2021). Thus, microbial communities can affect a species' competitive ability, host-to-host interactions, and ultimately, invasion success (Van Der Heijden et al., 2006; Lin et al., 2015; Tedersoo et al., 2020).

In particular, microbial transmission from native to invasive ('symbiont spillback') or from invasive to native hosts ('symbiont spillover') can lead to the establishment or disruption of host-symbiont associations and alter invasive trajectories in several ways (Bever et al., 2010; Dickie et al., 2017; Martignoni and Kolodny, 2023). For example, the formation of novel associations between invasive plants and pre-existing native mycorrhizal networks can

18 facilitate the establishment of an introduced host population and its expansion into a new
19 range (Dawkins and Esiobu, 2016; Parepa et al., 2013; Moeller et al., 2015). Analogously,
20 the spillover of parasites or pathogens from invasive to native hosts can weaken a native
21 population, and eventually lead to its extinction (Panzavolta et al., 2021; Santini et al., 2013;
22 Grünwald et al., 2012; Schuchert et al., 2014). Microbially mediated effects can also provide
23 resilience to native communities. For instance, host invasiveness may be decreased by a
24 reduction in the abundance of invasive symbionts (Zenni and Nuñez, 2013; Catford et al.,
25 2009), or by the transmission of pathogenic agents from native to invasive hosts (Mordecai,
26 2013; Flory and Clay, 2013).

27 Awareness of microbially mediated invasion (also termed ‘linked invasion’, see Dickie et al.
28 (2017)) is growing rapidly, and so are attempts at its conceptualization (Dickie et al., 2017;
29 Amsellem et al., 2017). Conceptual frameworks have focused on the impact of pathogenic
30 and mutualistic microbes on invasion (Dunn and Hatcher, 2015; Médoc et al., 2017; Mitchell
31 et al., 2006; Nuñez et al., 2009), or have aimed to integrate these two directions and examined
32 similarities of microbially mediated invasion occurring when shared microbes are pathogenic
33 or mutualistic (Dickie et al., 2017). While experimental studies are flourishing, ecological
34 population modelling has mostly studied the range expansion and invasion dynamics of either
35 parasites (White et al., 2018; Gubbins et al., 2000), or host populations (Lewis et al., 2016),
36 largely neglecting the importance of host-microbial feedback on the invasion dynamics (but
37 see Martignoni et al. (2020a); Yamauchi et al. (2011); Jack et al. (2017); Martignoni et al.
38 (2020c); Martignoni and Kolodny (2023)).

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 mostly
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 derived by 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 may help identify common features of mutualistic
47 or host-parasite networks, and test hypotheses regarding the relationship between structure
48 and community-wide dynamics (Valdovinos, 2019; Bascompte and Olesen, 2015). However,
49 particularly for the case of mutualistic networks, analyses have been performed on commu-
50 nities of free-living species, such as pollination or seed-dispersal mutualisms (Bascompte and

Glossary

Microbial invasion: Biological invasion of microbial agents.

Microbially mediated invasion: Biological invasion facilitated by microbial agents. The invasive organisms may be introduced host species, introduced microbial species, or both host and microbial species engaged in a symbiotic relationship.

Microbial sharing: The exchange of microbial agents between native and invasive hosts. The exchanged microbes may be beneficial or harmful to the new host.

Co-invasion: Simultaneous invasion of introduced hosts and their microbial symbionts.

Symbiont spillover: The transmission of introduced microbes from invasive to native hosts.

Symbiont spillback: The transmission of native microbes from native to invasive hosts.

Holocommunity: An ecological community comprising hosts species and their associated microbial symbionts, where microbial exchange between hosts of the same or different species can occur.

51 [Jordano, 2013](#)), whose dynamics may differ from what is observed in host-associated microbial
52 communities. Additionally, theoretical outputs are largely based on Lotka-Volterra equations
53 that may lead to inaccurate predictions due to their unrealistic biological assumptions, such as
54 linear positive effects of mutualistic interactions and unlimited growth ([Holland, 2015](#)). Thus,
55 the development of mathematical models that integrate biologically relevant mechanisms,
56 such as density-dependent (instead of linear) positive effects of mutualism, while maintain-
57 ing the necessary simplicity to allow analytical tractability, is key to providing a predictive
58 understanding of the dynamics of host-microbial communities and their invasibility.

59 We develop a mathematical framework to explore the possible invasion dynamics occurring
60 when native and invasive hosts may share their beneficial (i.e., mutualistic) and harmful (i.e.,
61 parasitic or pathogenic) microbes. Our model accounts for key features of host-symbiont in-
62 teractions including, critically, host-symbiont interdependent fitness and horizontal microbial
63 transmission between hosts. Our analysis allows us to disentangle different factors influencing
64 the community dynamics, such as each species' competitive ability and the resource exchange
65 capacity between hosts and symbionts, with our main goal being to understand how changes
66 in growth rates driven by novel microbial associations affect invasion success.

67 Despite their opposite effects on host fitness, invasion dynamics driven by beneficial mi-
68 crobes or harmful microbes may present similar interaction motifs ([Dickie et al., 2017](#)). For
69 instance, the formation of mutualistic associations between invasive hosts and native mycor-
70 rhizal fungi (i.e., an association that would benefit invasive hosts) and the transmission of
71 invasive pathogens to native hosts (i.e., an association that may weaken native hosts) may
72 lead to similar outputs, namely providing a competitive advantage to invasive hosts and in-
73 creasing their invasion success. Our model characterization allows us to identify and organize
74 these unifying patterns of microbially mediated invasion through the exploration, within a
75 single framework, of dynamics occurring when microbial influence on host growth may range
76 from beneficial to harmful, depending on the balance between the benefits and costs of the
77 association.

78 We will describe multiple microbially driven dynamics that may result in no invasion, in
79 co-invasion (defined here as the simultaneous invasion of an introduced host population and
80 its microbial community), or in either host or microbial invasions. We portray the model in
81 terms that correspond best to symbioses for which microbes are primarily external to their
82 hosts (e.g., plant-microbial symbioses), because these have been studied and described ([Dickie
83 et al., 2017](#); [Bever et al., 2010](#)). However, the same principles hold for systems in which the
84 microbes are internal or partially internal to their hosts (e.g., gut or coral microbiomes, [Pettay
85 et al. \(2015\)](#); [Chiarello et al. \(2022\)](#); [Goedknecht et al. \(2017\)](#)).

86 **2 Model and Methods**

87 **2.1 Mathematical framework**

88 To investigate the dynamics of host-microbial communities we develop a consumer-resource
89 model for mutualism ([Holland and DeAngelis, 2010](#)), similar to that presented by [Martignoni
90 et al. \(2020b\)](#). We consider a native host population with biomass p_n and its associated native
91 microbial community with biomass m_n . Hosts and microbes interact by exchanging resources
92 necessary for each other's growth. For example, in the case of the mycorrhizal symbiosis, the
93 host plant may provide synthesized carbon in the form of sugars (e.g., glucose and sucrose) to
94 its associated mycorrhizal fungi, and receive necessary nutrients such as phosphorus, nitrogen,
95 or water in return ([Smith and Read, 2010](#)). The transfer of resources from hosts to microbes
96 increases microbial biomass and decreases host biomass. The transfer of resources from mi-

97 crobes to hosts increases host biomass and decreases microbial biomass. We consider hosts
 98 to be facultative mutualists, and capable of some growth in the absence of microbes (with
 99 intrinsic growth rate quantified by the parameter r_p), while microbes are obligate mutualists
 100 and can not grow in the absence of a host. We then extend this model to include interactions
 101 between an invasive host population (with biomass p_i) and its microbial community (with
 102 biomass m_i). We consider that native microbes may exchange resources with native hosts,
 103 and invasive microbes may exchange resources with native hosts. Competition between native
 104 and invasive hosts (c_p parameters) and between native and invasive symbionts (c_m param-
 105 eters), may reduce their abundance, e.g., due to competition for host colonization between
 106 microbes (Engelmoer et al., 2014; Smith et al., 2018), or due to host competition for light or
 107 other external resources (Craine and Dybzinski, 2013).

We obtain the following equations:

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

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

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

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

108 All of the parameters and the functions f are discussed in detail below. A schematic
 109 representation of this model is provided in Fig. 2.

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

121 To explore the effect of microbial sharing on invasion success, we consider that parameters
 122 α_{in} , α_{ni} , β_{in} and β_{ni} can be zero or positive, depending on whether or not resource exchange
 123 between invasive microbes/hosts and native hosts/microbes is occurring. If invasive hosts
 124 exchange nutrients with native microbes, parameters α_{ni} (quantifying the resource supply from
 125 native microbes to invasive hosts) and β_{in} (quantifying the resource supply from invasive hosts
 126 to native microbes) will assume positive values. The relationship between how much a host
 127 receives from its associated microbes (which depends on α parameters) and how much a host
 128 gives to its associated microbes (which depends on β parameters) per unit time determines
 129 whether a host-microbial relationship is beneficial or harmful for the host. Generally, the
 130 relationship is beneficial for $\alpha \simeq \beta$, and harmful for $\alpha \ll \beta$. A thorough explanation of
 131 the quantitative criteria used to understand whether the exchange is beneficial or harmful is
 132 provided below in the ‘Harmful and beneficial microbes’ section.

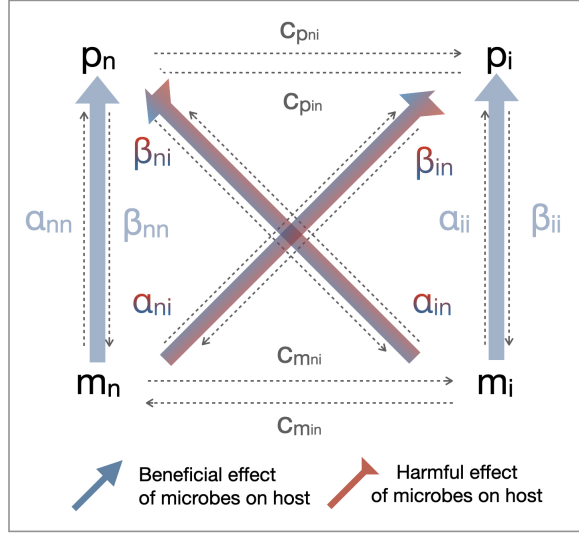


Fig. 1: Schematic representation of the model of Eq. (1). A native microbial community m_n is associated with a host population p_n . Resource exchange between hosts and microbes is quantified by parameters α_{nn} (microbes to hosts) and β_{nn} (hosts to microbes). Similarly, a population of invasive hosts p_i exchanges resources with its associated invasive microbial community m_i (parameters α_{ii} and β_{ii}). Depending on the scenario considered, invasive hosts can also exchange resources with native microbes, and so do invasive microbes with native hosts (parameters α_{in} , α_{ni} , β_{in} and β_{ni}). Blue and red arrows indicate whether resource exchange is beneficial or harmful to the host. Additionally, native and invasive hosts compete with each other, with competition strength quantified by parameters c_{pin} and c_{pni} , and so do native and invasive microbes (parameters c_{min} and c_{mni}).

133 In addition to resource exchange parameters, resource supply also depends on host and
 134 microbial densities, as determined by the functions f_m and f_p . Functions f_m^{jk} are the density-
 135 dependent rates at which the microbial community m_j supplies resources to the host popula-
 136 tion p_k (or the rates at which a host population p_k receives resources from m_j), with indexes
 137 $j = n, i$ and $k = n, i$ referring to native (n) or invasive (i) populations. Functions f_p^{jk} refer
 138 to the density-dependent rates at which the host population p_j supplies resources to the mi-
 139 crobial community m_k (or the rates at which the microbial community m_k receives resources
 140 from the host population p_j). We define:

$$141 \quad f_m^{jk} = \frac{m_j p_k}{dm_j + dm_k + p_k + p_j} \quad \& \quad f_p^{jk} = \frac{p_j m_k}{p_j/d + p_k/d + m_k + m_j}. \quad (2)$$

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

$$152 \quad f_p^{jk} \simeq \begin{cases} p_j \frac{m_k}{m_k + m_j} & \text{if } m_k + m_j \gg (p_j + p_k) \frac{1}{d}, \\ m_k d \frac{p_j}{p_j + p_k} & \text{if } m_k + m_j \ll (p_j + p_k) \frac{1}{d}. \end{cases} \quad (3)$$

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

$$157 \quad f_m^{jk} \simeq \begin{cases} m_j \frac{p_k}{p_k + p_j} & \text{if } p_k + p_j \gg (m_j + m_k)d, \\ \frac{p_k}{d} \frac{m_j}{m_j + m_k} & \text{if } p_k + p_j \ll (m_j + m_k)d. \end{cases} \quad (4)$$

158 2.2 Harmful and beneficial microbes

159 In our model, microbial contribution to host growth varies along a continuum ranging from
 160 ‘harmful’ to ‘beneficial’, depending on whether the additional presence of a given microbe
 161 increases or decreases host biomass at equilibrium (see Fig. 2). A native symbiont m_n is
 162 considered beneficial for an invasive host population if the host biomass at equilibrium p_i^*
 163 satisfies

$$164 \quad p_i^*(m_i(\alpha_{ii}), m_n(\alpha_{ni})) > p_i^*(m_i(\alpha_{ii}), 0), \quad (5)$$

165 and is considered harmful otherwise. An equivalent equation can be written to determine
 166 whether association with invasive microbes m_i is beneficial or harmful to native hosts p_n ,
 167 depending on the value of α_{in} .

168 The threshold distinguishing between beneficial and harmful microbes is determined by
 169 the value of $\alpha_{ni} = \alpha_{ni}^*$ for which equality in Eq. (5) is obtained. The value of α_{ni}^* depends on
 170 whether native symbionts are more or less beneficial than invasive symbionts (i.e., it depends
 171 on the value of α_{ii} , which is 0.4 in Fig. 2), and more generally, it depends on host biomass
 172 at equilibrium before and after the introduction of the new symbiont (as determined by all
 173 model parameters, see SI, section B).

174 If we fix the rate at which resources are transferred from hosts to symbionts (i.e., parameter
 175 β_{ni} or β_{in}), and consider only variations in the rate at which symbionts transfer resources to
 176 their hosts (i.e., variations in parameters α_{in} or α_{ni} , see Fig. 2), the value of α_{ni}^* satisfies the
 177 estimate

$$178 \quad \frac{q_{cp}}{q_{hp}} \beta_{in} d < \alpha_{ni}^* < \alpha_{ii} \quad (6)$$

179 (see SI C.3 and Fig. C.2 for the mathematical derivation of Eq. (6) and Eq. (21) for an
 180 accurate approximation of α_{ni}^*). In our analysis, we will consider the continuum of harmful
 181 to beneficial interactions ranging from $\alpha_{ni}, \alpha_{in} = 0$ to $\alpha_{ni} = \alpha_{nn}$ and $\alpha_{in} = \alpha_{ii}$ respectively
 182 (see SI, section C.3). Specific scenarios considered are provided in Table 1.

183 Finally, note that variations in the amount of resource supplied by hosts to microbes
 184 (implemented in the model through variations in parameters β_{in} and β_{ni}) could also be used
 185 to determine whether host associations are harmful or beneficial to microbes. Thus, we
 186 recognize that by considering only how microbes are harmful or beneficial to host, our analysis
 187 is fundamentally host-centric. This is done, however, in order to simplify the presentation of
 188 our results.

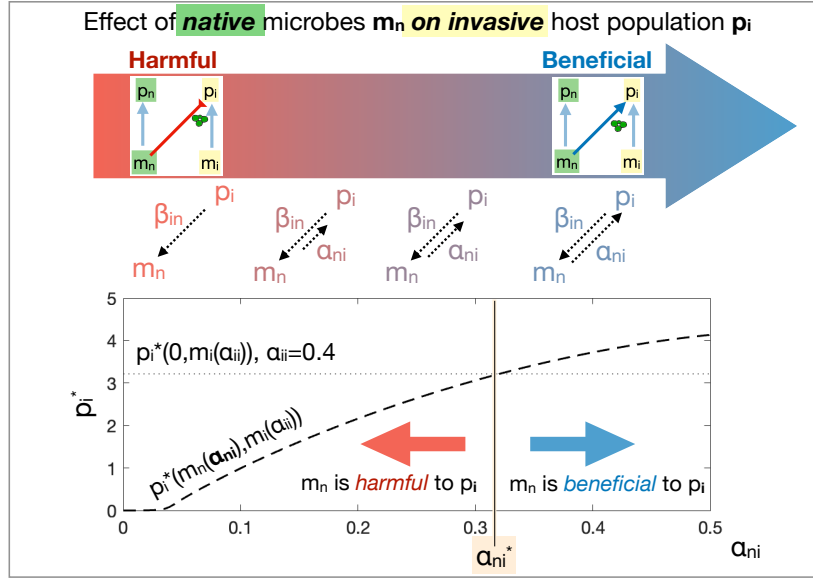


Fig. 2: The direct effect of a native microbial community m_n on an invasive host population may range from harmful (in red) to beneficial (in blue). We can explore this range by varying parameter α_{ni} , which quantifies the benefit provided by native microbes to invasive hosts, while all other parameters are kept constant (top right figure). The value of α_{ni}^* determines the threshold at which the microbial contribution switches from beneficial to harmful (or vice-versa), and is determined by the biomass of invasive hosts at equilibrium p_i^* in the absence of native microbes (bottom right figure). Equivalent results can be obtained when varying parameter α_{in} and considering the direct effect of invasive microbes m_i on native hosts p_n .

189 2.3 Model analysis

Interaction Scenario	Parameter values
(-, +)	$\alpha_{in} = 0, \beta_{ni} = \beta$; $\alpha_{ni} = \alpha, \beta_{in} = \beta$
(0, +)	$\alpha_{in} = 0, \beta_{ni} = 0$; $\alpha_{ni} = \alpha, \beta_{in} = \beta$
(+, +)	$\alpha_{in} = \alpha, \beta_{ni} = \beta$; $\alpha_{ni} = \alpha, \beta_{in} = \beta$
(-, 0)	$\alpha_{in} = 0, \beta_{ni} = \beta$; $\alpha_{ni} = 0, \beta_{in} = 0$
(0, 0)	$\alpha_{in} = 0, \beta_{ni} = 0$; $\alpha_{ni} = 0, \beta_{in} = 0$
(+, 0)	$\alpha_{in} = \alpha, \beta_{ni} = \beta$; $\alpha_{ni} = 0, \beta_{in} = 0$
(-, -)	$\alpha_{in} = 0, \beta_{ni} = \beta$; $\alpha_{ni} = 0, \beta_{in} = \beta$
(0, -)	$\alpha_{in} = 0, \beta_{ni} = 0$; $\alpha_{ni} = 0, \beta_{in} = \beta$
(+, -)	$\alpha_{in} = \alpha, \beta_{ni} = \beta$; $\alpha_{ni} = 0, \beta_{in} = \beta$

Table 1: 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. 3 (described in more detail in Fig. A.1). The first entry in each ordered pair indicates the effect of invasive microbes on a native hosts (which can be harmful ‘-’, neutral ‘0’, or beneficial ‘+’). The second entry indicates the effect of native microbes on an invasive hosts.

190 To highlight possible outcomes of the model (Eq. (1)), we will consider different scenarios,
 191 each one labeled with a coordinate pair, where the first entry in each ordered pair indicates the
 192 effect of invasive microbes on an native host population (which can be harmful ‘-’, neutral ‘0’,
 193 or beneficial ‘+’) and the second entry indicates the effect of native microbes on an invasive
 194 host population. The two entries categorise the coloured arrows in Fig. 1: The sign (negative,

195 zero, or positive) corresponds to the colour (red to blue) of the diagonal arrow. Fig. A.1
196 provides an illustrative overview of these scenarios.

197 There are, of course, many factors that can affect invasion success (Theoharides and
198 Duker, 2007; Heger and Trepl, 2003), and our framework can be readily used to explore the
199 relative importance of these factors through numerical simulations. In order to keep the focus
200 on microbially mediated invasion, however, the analysis we present here will consider the
201 acquisition of beneficial or harmful microbes as the primary factor influencing the community
202 dynamics. We will therefore discuss cases in which native and invasive species are characterised
203 by exactly the same parameters, except for variation in the value of the microbial sharing
204 parameters α_{ni} , α_{in} , β_{in} and β_{ni} (diagonal arrows in Fig. 1). We focus on situations in which
205 competition between hosts and competition between symbionts is strong. In these cases,
206 neither native and invasive hosts nor native and invasive symbionts can stably coexist, and
207 thus these scenarios are those most likely to be of concern for biological conservation. The
208 default values for the resource exchange parameters used in the different interaction scenarios
209 we consider are provided in Table 1. The default values of all other parameters are provided in
210 Table A.1. In SI I.2, we discuss how the strength of competition between hosts and symbionts
211 can affect observed outcomes.

212 When the effect of invasive microbes on native hosts is the same as the effect of native
213 microbes on invasive hosts (e.g., when the cross-species influence of invasive/native microbes
214 on native/invasive hosts is the same, as in scenarios $(-, -)$ and $(+, +)$, or when the native
215 and invasive hosts do not share microbes at all, as in scenario $(0, 0)$) microbial exchange
216 does not provide a competitive advantage to either native or invasive species. In these cases,
217 differences in other traits or drift (not considered in this model) will eventually cause one
218 host-microbe combination to take over the other. Trait differences between native and invasive
219 species may include: differences in the competitive effect of one species on another ($c_{m_{jw}}$ and
220 $c_{p_{jw}}$ parameters), differences in the rate of host-microbial resource exchange (α_{jw} and β_{jw}
221 parameters), differences in the efficiency by which nutrients supplied or received are converted
222 into biomass (q_{hp_j} , q_{cp_j} , q_{cm_j} , and q_{hm_j} parameters), differences in the intrinsic growth rate of
223 the hosts (r_{p_j} parameter), differences in maintenance costs (μ_{p_j} and μ_{m_j} parameters), which
224 can be related, for example, to the ability of a species to tolerate stress, or differences in initial
225 biomass. We call these differences ‘secondary effects’, as we consider that their effect on the
226 community dynamics is secondary to microbial acquisition. This is done, as explained before,
227 in order to focus on the direct effects of the microbial exchange.

228 3 Results

229 3.1 Overview of interaction scenarios

230 In the absence of competition, host and microbial biomass increase asymptotically over time
231 until a certain equilibrium value is reached. When considering a single host-symbiont pair, the
232 value of this equilibrium is derived in SI B, Eq. (12). A graphical representation of host and
233 microbial biomass at equilibrium in a single host-symbiont pair is provided in the phase-plane
234 of Fig. B.1. If we consider that multiple microbes can associate with multiple hosts, and
235 that symbionts are beneficial to the host, host biomass at equilibrium tends to increase with
236 increasing number of associated symbionts. This relationship can be shown by computing
237 host biomass at steady state as a function of the number of associated symbionts (see SI C,
238 Eqs. (18) and Fig. C.1). Indeed, in Fig. 2 we observe that host biomass at steady state is
239 higher for hosts associating with two symbionts, as long as both symbionts are beneficial to
240 the host (i.e., as long as $\alpha_{ni} > \alpha_{ni}^*$). Similarly, microbial biomass increases when microbes as-

241 sociate with multiple hosts. Thus, hosts/symbionts associating with more than one beneficial
242 symbiont/host are provided with a competitive advantage over hosts/symbionts associating
243 with only one beneficial symbiont/host.

244 This type of competitive advantage plays out in the scenarios of Fig. 3. For example,
245 in scenario $(0, +)$ (top row, middle column), the association of invasive hosts with native
246 microbes provides a competitive advantage to invasive hosts, as well as to native microbes.
247 The competitive exclusion dynamics that occur will vary depending on which of the following
248 events occurs first: native symbionts outcompeting invasive symbionts, or invasive hosts out-
249 competing native hosts (see Fig. 4a). Similarly, in scenario $(+, 0)$, the association of native
250 hosts with invasive microbes provides a competitive advantage to invasive microbes and native
251 hosts (Fig. 4b).

252 In scenarios $(-, 0)$ and $(-, +)$ of Fig. 3, we consider that the acquisition of invasive mi-
253 crobes that are harmful to native hosts provides a competitive advantage to invasive hosts.
254 In contrast, in scenarios $(0, -)$ and $(+, -)$, native microbes are harmful to invasive hosts, and
255 thus provide resilience against invasion.

256 In scenarios $(-, -)$, $(0, 0)$ and $(+, +)$ neither the hosts nor the microbes have a competi-
257 tive advantage over the other species due to microbial sharing, as both hosts have microbial
258 partners that provide the same benefit or cost. The coexistence equilibrium is unstable, as
259 we consider the case in which competition between hosts and microbes is strong, and which
260 species will be excluded will be determined by secondary effects, as explained at the end of
261 the ‘Model analysis’ section.

262 Note that the outcomes presented in Fig. 3 are only those that occur at the extreme ends
263 of a continuum of beneficial to harmful interactions (for which α parameters are equal to zero,
264 when microbes are harmful, or assume a fixed positive value, when microbes are beneficial,
265 see Table 1 and section ‘Harmful and beneficial microbes’). Exploration of specific scenar-
266 ios along this continuum, as well as specific scenarios corresponding to different parameter
267 combinations, can be conducted through numerical simulations of Eq. (1). A user-friendly
268 version of the code is made publicly available on the modelRxiv platform (Harris et al., 2022)
269 (<https://modelrxiv.org/model/YfndNX>), and can be used for this purpose. In SI I we also
270 provide more details on the outcomes of each scenario depending on parameter values, espe-
271 cially on different outcomes observed when varying the competitive effect of one species on
272 another (i.e., the magnitude of the c parameters), or the degree of mutualism of the host (from
273 obligate to facultative). Interesting emerging scenarios will be discussed in the next section.

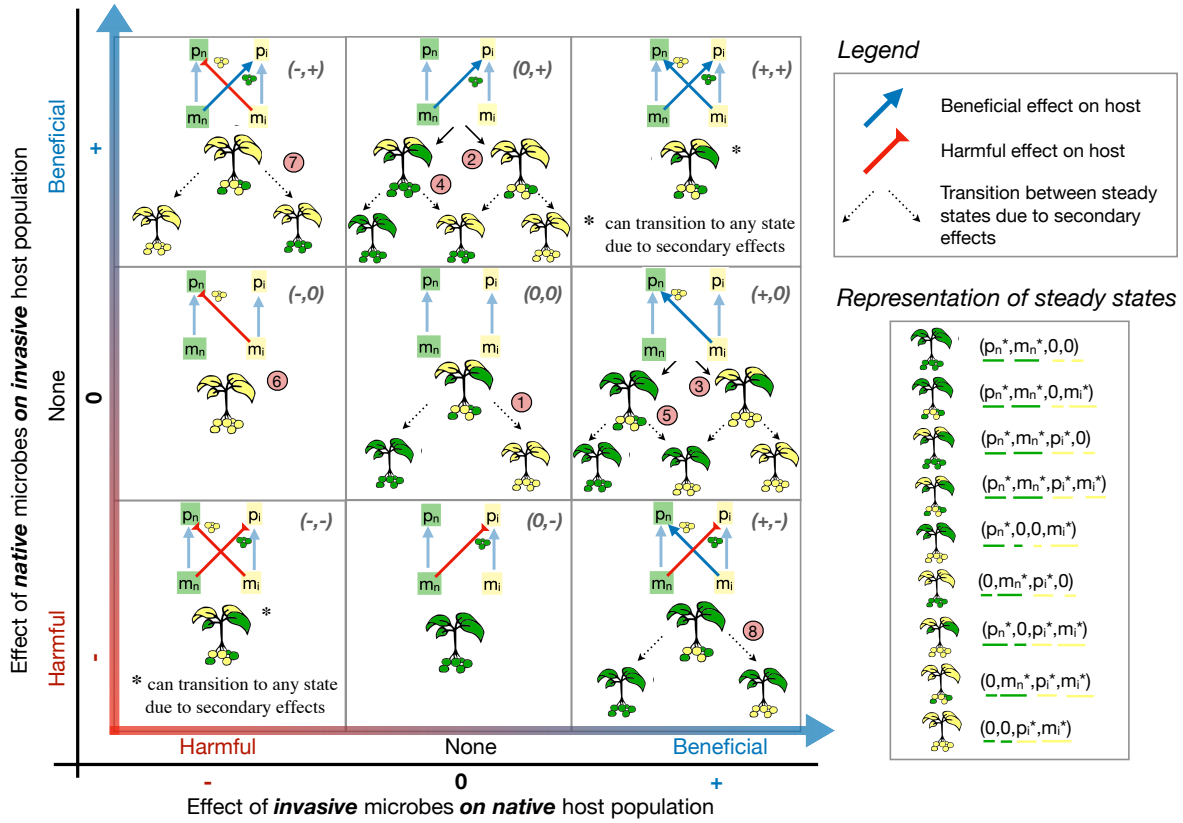


Fig. 3: Possible microbially mediated invasion dynamics occurring when native and invasive species share their beneficial or harmful microbes. The horizontal axis represents the effect of invasive microbes on native hosts (which can be harmful ‘-’, neutral ‘0’, or beneficial ‘+’), while the vertical axis represents the effect of native microbes on invasive hosts. The cell content represents the expected steady state in each scenario, where persistence of natives is represented by green icons (plants or microbes), while persistence of invaders is represented by yellow icons. Each cell is labeled with a coordinate pair, where the first entry in each ordered pair indicates the effect of invasive microbes on a native host population and the second entry indicates the effect of native microbes on an invasive host population. The resource exchange parameters corresponding to each scenario are provided in Table 1. The red numbered circles indicate eight possible microbially mediated pathways of invasion, which will be discussed in detail in the results section. Interactive reproduction and re-parametrization of these scenarios can be done through the modelRxiv platform (<https://modelrxiv.org/model/YfndNX>).

274 3.2 Dynamics of microbially mediated invasion

275 Here we discuss eight possible microbially mediated invasion dynamics emerging from our
 276 analysis, and numbered according to the invasion pathways shown in Fig. 3. This analysis is
 277 not exhaustive, but rather is intended to highlight several possible dynamics that can lead to
 278 invasion of hosts, microbes, or both, and in particular illustrate that several routes can lead
 279 to each outcome despite differences in underlying mechanisms.

280 **① Co-invasion via no microbial sharing:** When no microbial sharing occurs, competi-
 281 tive exclusion of one host-symbiont community, either the native or the invasive one, occurs
 282 through selection due to trait differences or differences in initial abundance, or through drift
 283 (not considered here). When selection due to trait differences occur, the host-microbial asso-
 284 ciations that provides the highest fitness to either hosts or symbionts outcompete the other.
 285 Highest fitness can be provided through ‘secondary effects’, such as differences in the competi-
 286 tive effect of one species on another, or differences in stress tolerance, as explained at the end

287 of the ‘Model analysis’ section. The quality of resource exchange between hosts and symbionts
288 can also be directly related to their competitive ability, as it determines their interdependent
289 growth rates.

290 Differences in initial abundance can also favor one host-symbiont community with respect
291 to the other. In classical theory, initial abundances do not affect the competitive dynamics of
292 two species, and if two competing species have the same competitive ability, each of the species
293 will fill in a proportion of the carrying capacity proportional to their initial abundance (Gilad,
294 2008). However, in host-symbiont communities, feedback loops induced by nutrient exchanges
295 affect such dynamics (see SI I.2.1 and SI I.1.4 for details). Differences in the initial abundance
296 of symbionts (or hosts) affect host (or symbiont) growth rate and, in turn, symbiont (or host)
297 growth rate, providing a competitive advantage to the community with the largest abundance
298 of hosts or symbionts.

299 **② Co-invasion via spillback of beneficial microbes:** Association with beneficial native
300 microbes may provide a competitive advantage to invasive hosts that leads to competitive
301 exclusion of native hosts (Fig. 4a, right pathways, and SI I.2.4 for details). Subsequently,
302 invasive symbionts may outcompete native symbionts, e.g., if native symbionts are weakened
303 by the absence of native hosts or if invasive symbionts are empowered by an increase in invasive
304 hosts (Fig. 4a, far right pathway, leading to association between p_i and m_i). Alternatively,
305 invasive symbionts may be outcompeted by native symbionts (Fig. 4a, centre right pathway,
306 leading to association between p_i and m_n).

307 In the absence of microbial sharing, less mutualistic host-microbial associations have lower
308 fitness with respect to more mutualistic host-microbial associations, and are thus not likely
309 to invade (as discussed in ①). When microbial sharing can occur, however, co-invasion can
310 be driven by the exploitation of existing host-microbial associations. For example, if invasive
311 symbionts are less beneficial toward native hosts than native symbionts (i.e., $\alpha_{\alpha_{in}} < \alpha_{nn}$, see
312 also point ⑥), or if hosts are less beneficial toward native symbionts than native hosts (e.g.,
313 $\beta_{in} < \beta_{nn}$), invasive hosts indirectly exploit native hosts, by receiving resources from native
314 symbionts at low cost.

315 This particular dynamic is highlighted in Fig. 5a: Introduced invasive hosts may grow
316 rapidly by benefiting from the presence of a large native microbial community and, indirectly,
317 from their native hosts. Consequently, native hosts and symbionts suffer from the presence of
318 invasive hosts and experience a reduction in biomass. Eventually, the increase in the biomass
319 of invasive hosts also increases the biomass of invasive symbionts, which grow larger than
320 native symbionts and outcompete them. Subsequently, in the absence of native hosts and
321 symbionts, the biomass of invasive hosts decreases (as they can no longer acquire resources at
322 little cost), and co-invasion leads to a community that has lower biomass.

323 **③ Co-invasion via spillover of beneficial microbes:** In this scenario, mutualistic asso-
324 ciation of invasive microbes with native hosts provides a competitive advantage to invasive
325 microbes, that then outcompete native microbes (Fig. 4b, right pathways, and SI I.2.4 for
326 details). The disruption of the association between native hosts and their symbionts may
327 weaken native hosts, and lead to invasive host establishment. Thus, in this case, co-invasion
328 may be observed due to symbiont spillover (Fig. 4b far right pathway, leading to association
329 between p_i and m_i). Alternatively, microbial invasion may be observed if invasive hosts are
330 outcompeted by native hosts, but invasive symbionts persist in association with native hosts
331 (Fig. 4b centre right pathway, leading to association between p_n and m_i).

332 **④ Host invasion via spillback of beneficial microbes:** Here, mutualistic association with
333 invasive hosts provides a competitive advantage to native symbionts, that then outcompete

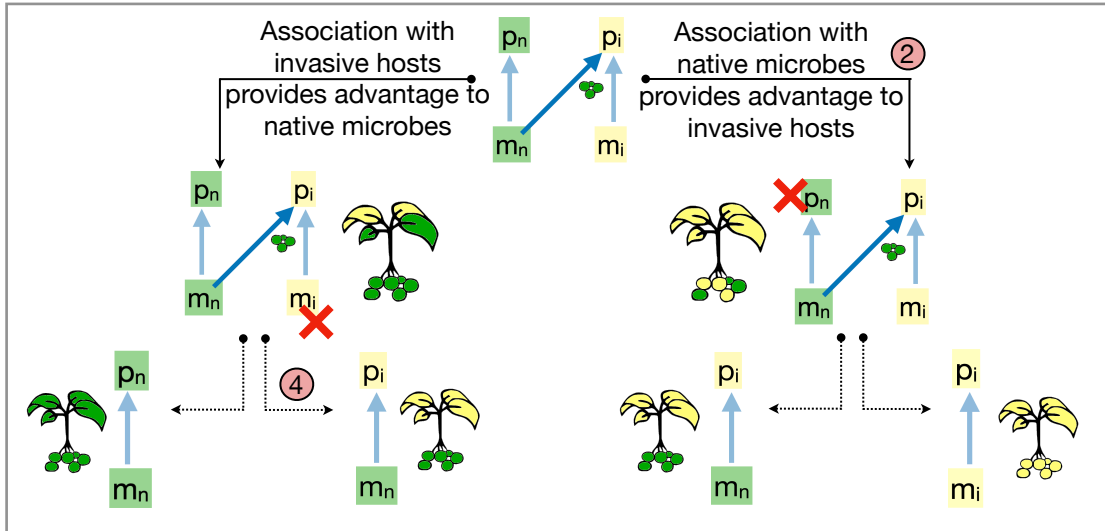
334 invasive symbionts (Fig. 4a, left pathway, and SI I.2.4 for details). Exclusion of invasive
335 symbionts may provide a competitive advantage to invasive hosts, and lead to the exclusion
336 of native hosts, particularly if invasive symbionts are low quality mutualists, or even parasitic
337 to their host (see Fig. B.3 for details on parasitic terminology). In this case, we observe the
338 formation of novel associations between invasive hosts and native symbionts (Fig. 4a centre
339 left pathway, leading to association between p_i and m_n). No invasion occurs if invasive hosts
340 suffer from the disruption of invasive host-symbiont associations which causes them to be
341 outcompeted by native hosts (Fig. 4a far left pathway, leading to association between p_n and
342 m_n).

343 **⑤ Microbial invasion via spillover of beneficial microbes:** In this case, association with
344 invasive symbionts provides an advantage to native hosts, that then outcompete invasive hosts
345 (Fig. 4b, left pathway and SI I.2.4 for details). If invasive symbionts are strong competitors,
346 they may subsequently exclude native symbionts, which would lead to the formation of novel
347 associations between invasive symbionts and native hosts, and to microbial invasion (Fig. 4b
348 centre left pathway, leading to association between p_n and m_i). Note that this scenario of
349 symbiont replacement may be more likely to occur, as it can be observed through two different
350 pathways, namely, the centre left and right pathways in Fig. 5b. If invasive microbes are less
351 mutualistic than natives, the substitution of native symbionts with invasive symbionts may
352 lead to a loss in the biomass of native hosts (Fig. 5b). In this situation, invasive microbes
353 continue to be present in the environment and negatively affect ecosystem functionality long
354 after the disappearance of their invasive hosts. No invasion occurs if invasive symbionts suffer
355 from the absence of invasive hosts and are outcompeted by native symbionts (Fig. 4b far left
356 pathway, leading to associations between p_n and m_n).

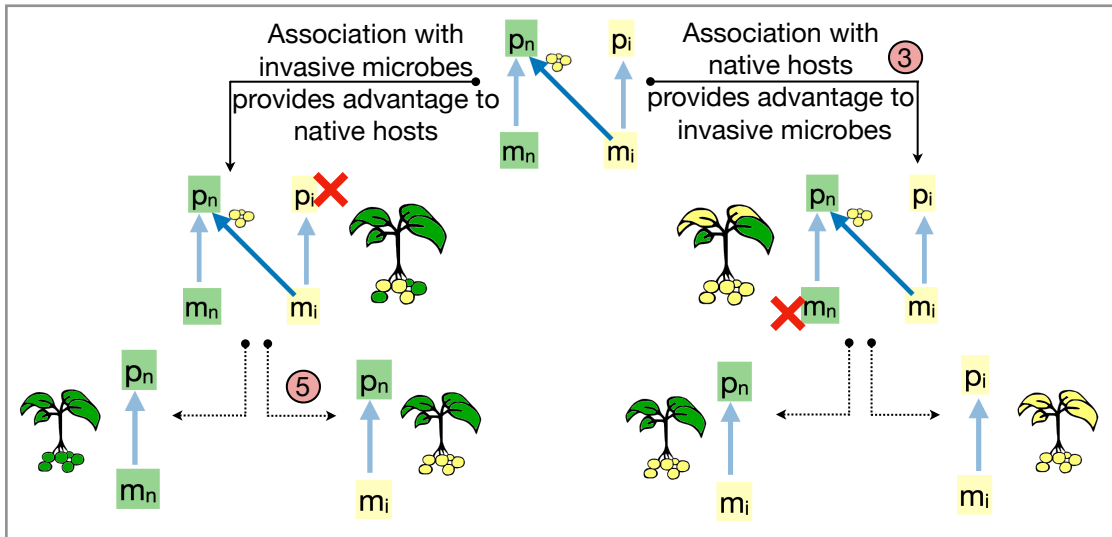
357 **⑥ Co-invasion via spillover of harmful microbes:** Co-invasion may be facilitated if
358 invasive symbionts are harmful to native species, which would weaken native hosts and cause
359 their competitive exclusion and the consequent exclusion of their symbionts (see SI I.2.3 for
360 further insights). This situation can occur, e.g., if pathogens causing disease in native hosts are
361 co-introduced with invasive hosts. A similar effect can also be observed if invasive symbionts
362 are less mutualistic than native symbionts, and exploit native hosts at the indirect expense
363 of native symbionts. Such a mechanism would weaken native host-symbiont communities and
364 lead to their competitive exclusion. The newly established invasive host-symbiont community
365 will subsequently experience a loss of biomass due to the disappearance of the native hosts
366 and symbionts that were being exploited, similar to what was observed in Fig. 5a.

367 **⑦ Host invasion via spillover of harmful microbes and spillback of beneficial mi-**
368 **crobes:** Microbial sharing may lead to the combined effect of increasing the fitness of inva-
369 sive hosts (through the formation of novel associations with native symbionts) and decreasing
370 the fitness of native hosts (through the acquisition of invasive parasites or pathogens), making
371 the dynamics of host invasion described in **②** more likely to occur (see SI I.2.2 for further
372 insights). Note that this scenario may also represent the situation in which both native and
373 invasive hosts can share microbes, but if some microbes are more mutualistic than others
374 the resulting system can transition from the scenario described in $(+, +)$, to either $(-, +)$ or
375 $(+, -)$.

376 **⑧ Microbial invasion via spillback of harmful microbes and spillover of beneficial**
377 **microbes:** The dynamics of microbial invasion described in **⑤** is more likely to occur if
378 native parasites are transmitted to invasive hosts, facilitating their competitive exclusion by



(a)



(b)

Fig. 4: More detailed insights into the possible dynamics highlighted in scenarios (a) (0, +) and (b) (+, 0) of Fig. 5. Association of native microbes with invasive hosts (or of invasive microbes with native hosts) may provide a competitive advantage to hosts or symbionts, where different outcomes are observed depending on whether hosts or microbes competitively exclude each other first.

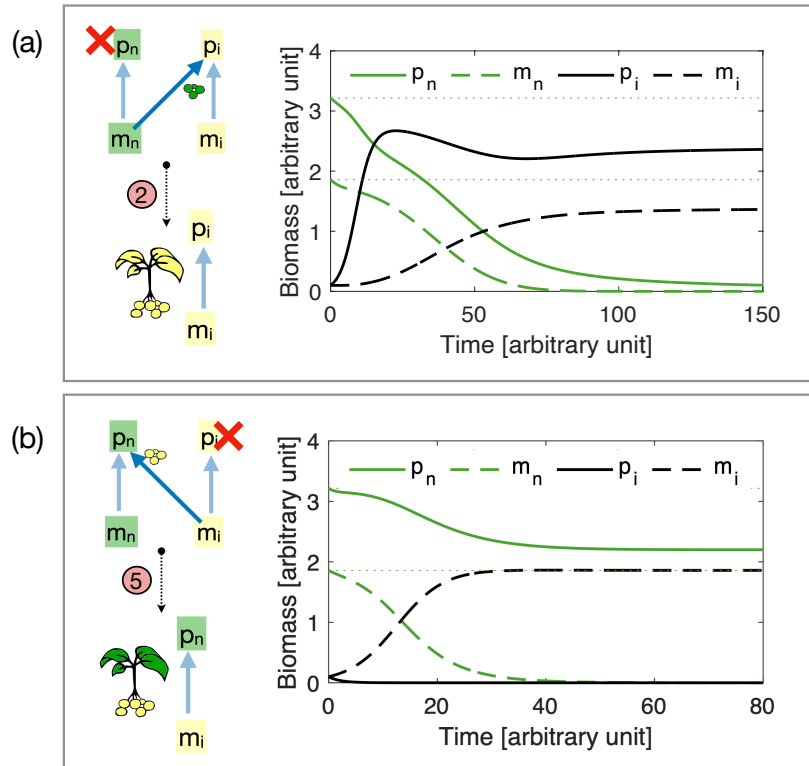


Fig. 5: (a) Possible dynamics of microbially mediated co-invasion occurring when native symbionts associate with less beneficial invasive hosts. These associations may lead to the indirect exploitation of native hosts, and to their competitive exclusion by invasive hosts. In turn, native symbionts may be weakened by the absence of native hosts, and be competitively excluded by invasive symbionts. In this case, the resulting community will have lower biomass with respect to the displaced invasive community (compare black curves and dotted green horizontal lines). (b) Possible dynamics of microbial invasion occurring when native hosts associate with less beneficial invasive symbionts. Again, the resulting community has lower biomass than the original community. Interactive simulation of these and related scenarios can be done through the modelRxiv platform (<https://modelrxiv.org/model/YfndNX>).

379 native hosts. Also in this case, invasive symbionts may persist in the environment by forming
 380 novel associations with native hosts (see SI I.2.2 for further insights).

381 4 Discussion

382 Microbial sharing between native and invasive species can facilitate invasion of introduced
 383 hosts or provide resilience to native communities. We present a framework that allows us to
 384 explore these outcomes systematically, and organize them along a continuum of harmful to
 385 beneficial host-microbial interactions.

386 4.1 Microbially mediated increase in invasion risk

387 A growing number of empirical studies, particularly on plant-fungal associations, have shown
 388 microbially mediated invasion can occur when invasive hosts form novel mutualistic associa-
 389 tions with native symbionts, eventually increasing a host competitive ability (Callaway et al.,
 390 2004; Tedersoo et al., 2007; Moeller et al., 2015; Shipunov et al., 2008). Strong evidence also
 391 shows that pathogens co-introduced with invasive hosts may weaken native host populations,
 392 which favours their competitive exclusion by invading hosts in a dynamic often referred to as

393 ‘disease-mediated invasion’ (Anderson et al., 2004; Parker and Gilbert, 2004; Desprez-Loustau
394 et al., 2007; Santini et al., 2013; Carnegie et al., 2016). We highlight the possibility that some
395 of these mechanisms may occur not only when shared symbionts are either pathogens or mu-
396 tualists, but also when the mutualistic quality of introduced symbionts differs from that of
397 native symbionts. For instance, introduced symbionts that are slightly less mutualistic than
398 those found in native communities might be perceived by native hosts as parasitic, as their
399 association with native hosts may lead to a decrease in biomass (Bever, 2002). A similar dy-
400 namics is observed if native acquire introduced pathogens, although the decrease in biomass
401 in this case should be to a lesser extent. Similarly, the acquisition of native symbionts that
402 are slightly more mutualistic than the original invasive community can lead to an increase in
403 the biomass of invasive hosts. These changes in population growth and abundance may not
404 be sufficient to directly drive a community to extinction (as for the acquisition of pathogenic
405 microbes), but they may be enough to provide a competitive advantage to a population with
406 respect to another and change the invasion dynamics (Levine et al., 2004).

407 In addition to highlighting the possible dynamics along the mutualism-parasitism contin-
408 uum, we would like to emphasize the importance of considering invasion dynamics arising
409 at the whole community level, rather than thinking in terms of host-symbiont pairs. Previ-
410 ous theoretical work has often considered host-symbiont pairs (i.e., ‘holobionts’) as units of
411 selection (Roughgarden et al., 2018; Gilbert et al., 2017; Zilber-Rosenberg and Rosenberg,
412 2008), which may lead to the misconception that only the host-symbiont pair that provides
413 the highest fitness to their host may co-invade and displace native communities, as observed
414 in some instances (Dickie et al., 2010; Nunez and Dickie, 2014; Hayward et al., 2015). How-
415 ever, when accounting for the possibility that symbiont disruption and exchange among native
416 and invasive hosts may occur (Dickie et al., 2017; Catford et al., 2009; Mitchell et al., 2006),
417 co-invasion of a less fit host-symbiont pair may be observed. We emphasize that when think-
418 ing of microbially mediated invasion it is important to move beyond the holobiont concept
419 (Douglas and Werren, 2016; Skillings, 2016; Morar and Bohannan, 2019), and reason in terms
420 of ‘holocommunity’, or host-symbiont communities. Accounting for higher-order interactions
421 between and among multiple hosts and symbionts is key to evaluating the whole range of
422 possible outcomes following the introduction of a new species (Dickie et al., 2017; Fahey and
423 Flory, 2022).

424 In some instances, microbially mediated invasion may lead to changes in total commu-
425 nity biomass with, in some circumstances, long-term repercussions on ecosystem functionality
426 (Nunez and Dickie, 2014; Lovett et al., 2006; Dickie et al., 2011; Mitchell and Power, 2003;
427 Cobb and Rizzo, 2016; Preston et al., 2016; Ehrenfeld, 2010). Although this reduction in com-
428 munity biomass is well-known for pathogen spread (Lovett et al., 2006; Mitchell and Power,
429 2003; Cobb and Rizzo, 2016; Preston et al., 2016), here we present alternative mechanisms
430 that can lead to an invasion-driven biomass decrease through higher-order interactions (Bil-
431 lick and Case, 1994; Mayfield and Stouffer, 2017). For example, if invasive hosts provide a
432 reduced reward as compared to natives (Hoffman and Mitchell, 1986; Mummey and Rillig,
433 2006; Hausmann and Hawkes, 2009; Vogelsang and Bever, 2009), associations between invasive
434 hosts and native symbionts will lead to the direct exploitation of the resources provided by
435 native symbionts. In addition, there will be indirect exploitation of more mutualistic native
436 hosts that invested resources in the growth of a large native microbial community from which
437 it can no longer fully benefit. Thus, in this case, an increase in the abundance of invasive
438 hosts occurs in conjunction with a decrease in the abundance of native symbionts and their
439 hosts (Fig. 5(a)) (Vogelsang and Bever, 2009).

4.2 Microbially mediated increase in community resilience

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

A clear example is the transmission of native pathogens to invasive plants (Hood et al., 2008; Piou et al., 2002), which can provide biotic resistance against invaders (Mordecai, 2013; Flory and Clay, 2013; Prev y and Seastedt, 2015). Other more complex dynamics of biotic resistance occur when native symbionts, which have co-evolved with native hosts, are highly mutualistic to native hosts but not to invasive hosts (Bunn et al., 2015; Moora et al., 2011). Thus, association with these symbionts can be perceived as slightly parasitic by invasive hosts, and can allow for their competitive exclusion by native hosts.

Finally, less competitive host-symbiont pairs may resist invasion by associating with mutualistic invasive symbionts (Mordecai, 2013; Flory and Clay, 2013). Although reports of mutualistic association between native hosts and invasive symbionts are limited, it is certain that these associations occur and, in some instances, provide natives with biotic resistance to invasives. Indeed, reports of native pathogenic transmission to invasive hosts are numerous (Anderson et al., 2004; Parker and Gilbert, 2004; Desprez-Loustau et al., 2007; Santini et al., 2013; Carnegie et al., 2016), and so are reports of symbiont spread in native habitats (Dickie et al., 2016; Wolfe and Pringle, 2012; Berch et al., 2017; Mallon et al., 2015; Hart et al., 2017). Thus, it is possible that the scant existing evidence for the establishment of novel mutualistic associations between native hosts and invasive microbes and their role in preventing invasion is due to reporting biases (Dickie et al., 2017). We hope that our insights will inspire further empirical studies aimed at evaluating the role of microbial association in contributing to invasion failure.

4.3 Framework limitations and possible extensions

In our work, we highlight some of the multiple possible theoretical scenarios of microbially mediated invasion, however it is important to understand that the feasibility of each scenario in practice needs to be assessed on a case-by-case basis. The specificity of host-symbiont interactions and variability in their contribution to host fitness is crucial to understanding which scenarios are more likely to occur in particular settings. In this sense, our framework can be regarded as a helpful tool to explore possible microbially mediated invasion dynamics. In particular, parametrization based on realistic biological scenarios may provide insights into possible outcomes through numerical simulations (e.g., through the tool we provide on the modelRxiv platform, Harris et al. (2022)). Future model parametrization may utilize phylogenetic or ecological similarity as predictors of the amount of microbial sharing (Vacher et al., 2010; Bufford et al., 2016; Parker et al., 2015; Gilbert and Parker, 2016; Davison et al., 2015), together with other traits related to the invasiveness and invasibility of native and invasive species (Hoeksema et al., 2020; Traveset and Richardson, 2014; Litchman, 2010), such as their dependence on the symbiosis (Vogelsang and Bever, 2009; Klironomos, 2003).

In addition to narrowing the gap between theory and experimental results, the framework

487 presented here also provides a strong basis for new theoretical extensions. For instance,
488 an extended version of Eq. (1) that accounts for associations between multiple hosts and
489 symbionts is presented in SI E, and could be used to investigate a situation in which changes
490 in the native community composition are observed after species' introduction (Bunn et al.,
491 2015; Moora et al., 2011). If we consider that a microbial community is composed of multiple
492 microbial strains, and if invasive hosts support only certain microbial strains with respect to
493 others (Callaway et al., 2001; Bever, 2002; Kohout et al., 2011), changes in the abundance
494 of different strains may ultimately affect the overall benefit that the community provides to
495 its host (Vandegrift et al., 2015; Moeller et al., 2015). Although this scenario can already
496 be modelled implicitly within our framework (e.g., by considering the overall effect of novel
497 associations of the new host before and after species introduction), more explicit modeling
498 efforts could account for the presence of multiple microbial communities m_j characterized by
499 different rates of resource supply α_j . Evolution of host-symbiont interactions may also be
500 taken into account (Lankau and Nodurft, 2013; Dror et al., 2019), such as the evolution of
501 host adaptation to pathogens (Thrall et al., 2002), as well as the possible coupling of trait
502 evolution with abiotic conditions such as nutrients or moisture availability, or anthropogenic
503 disturbance (Johnson, 1993; Endresz et al., 2015; Clavel et al., 2021).

504 Further work may also consider dynamics arising when invasive hosts actively disrupt
505 native host-symbiont associations, e.g. through the secretion of various compounds (Vogelsang
506 and Bever, 2009; Meinhardt and Gehring, 2012; Stinson et al., 2006). This feature can be
507 incorporated into the model by adding a term to Eq. (1) that accounts for reduced symbiont
508 growth in the presence of an introduced host population. Other added features may include
509 spatial effects, such as accounting for asymmetries in the dispersal strategies of hosts and
510 symbionts (Martignoni et al., 2023; Moeller et al., 2015; Nuñez et al., 2009). Finally, interesting
511 microbially mediated dynamics that we did not discuss here, but that may benefit from
512 explicit modelling, are cases in which association of invasive hosts with native pathogens that
513 increase in abundance on invasive hosts leads to increased colonization of native hosts (i.e.,
514 the 'parasite-spillback' mechanisms) (Flory and Clay, 2013; Strauss et al., 2012; Kelly et al.,
515 2009; Mangla et al., 2008; Day et al., 2016).

516 5 Concluding remarks

517 Microbial sharing can lead to scenarios ranging from increased invasion success to increased
518 community resilience, and identification of the biological mechanisms favoring one or the other
519 process is key to predicting invasion risk. We provide a tool to explore these outcomes within
520 a single framework and advance the conceptualization of microbially mediated invasion and
521 its theoretical basis. Our framework can guide the formulation of new hypotheses that remain
522 to be tested empirically, to provide innovative insights into invasive species management and
523 restoration strategies (Kowalski et al., 2015).

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A Numerical simulations

A.1 Overview of interaction scenarios

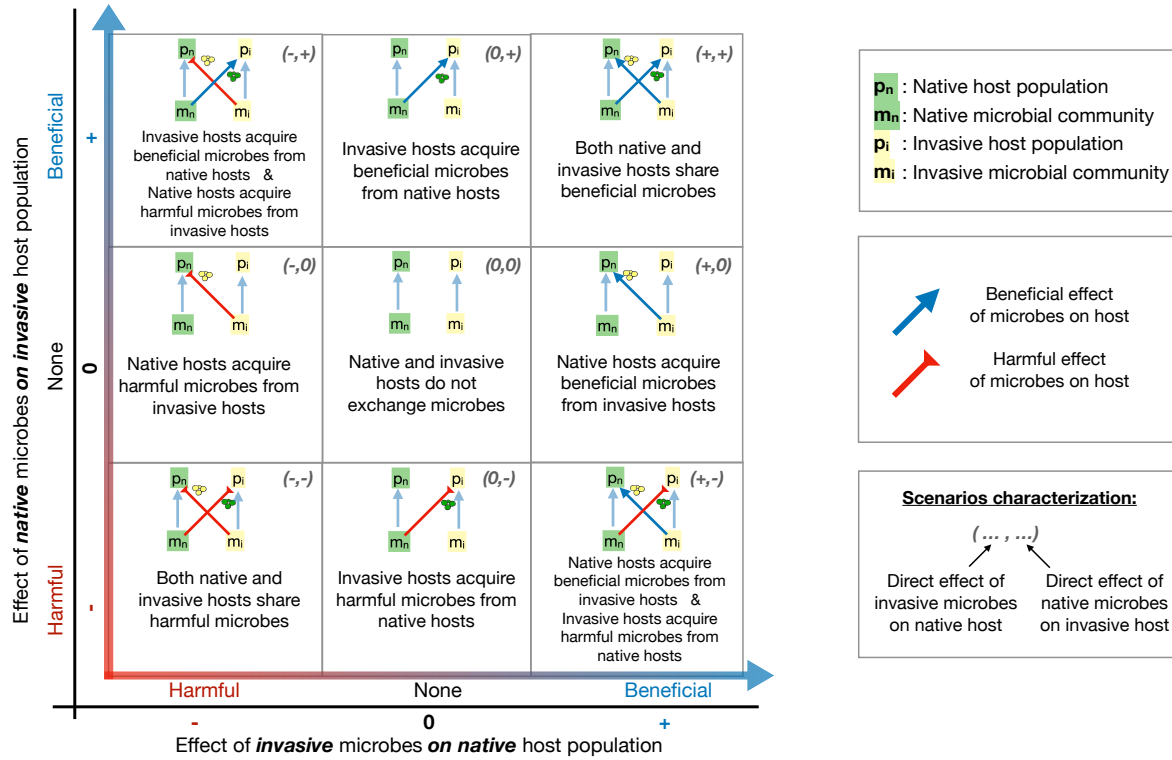


Fig. A.1: Overview of the interaction scenarios explored with the model. The horizontal axis represents the effect of invasive microbes on native hosts, while the vertical axis represents the effect of native microbes on invasive hosts. This effect can be negative ('-'), neutral ('0'), or positive ('+'), as represented by the diagonal arrows describing the interaction between invasive/native hosts with native/invasive microbes.

911 **A.2 Default parameter values**

912 A brief description of model parameters and their default values used for the simulations
 913 is provided in Table A.1. Specific parameters used for the plots in Fig. 5 are provided in
 914 Table A.2.

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. 5, as provided in Table A.2. Representative parameters for the interaction scenarios presented in Fig. 3 are provided in Table 1.

Figure	Parameter	Value	Figure	Parameter	Value
5a	α_{ii}	0.3	5b	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.2: Brief description of model parameters used to produce Fig. 5. Other parameter values corresponds to those listed in Table A.1.

915 **A.3 Scenarios of interest**

916 Scenarios of interest are uploaded on the modelRxiv platform, at the following link: [https://](https://modelrxiv.org/model/YfndNX)
917 modelrxiv.org/model/YfndNX. The website allows the reproduction and re-parametrization
918 of the 9 interaction scenarios of Fig. 3, as shown in Fig. A.2, and the interactive reproduction
919 of Fig. 5.

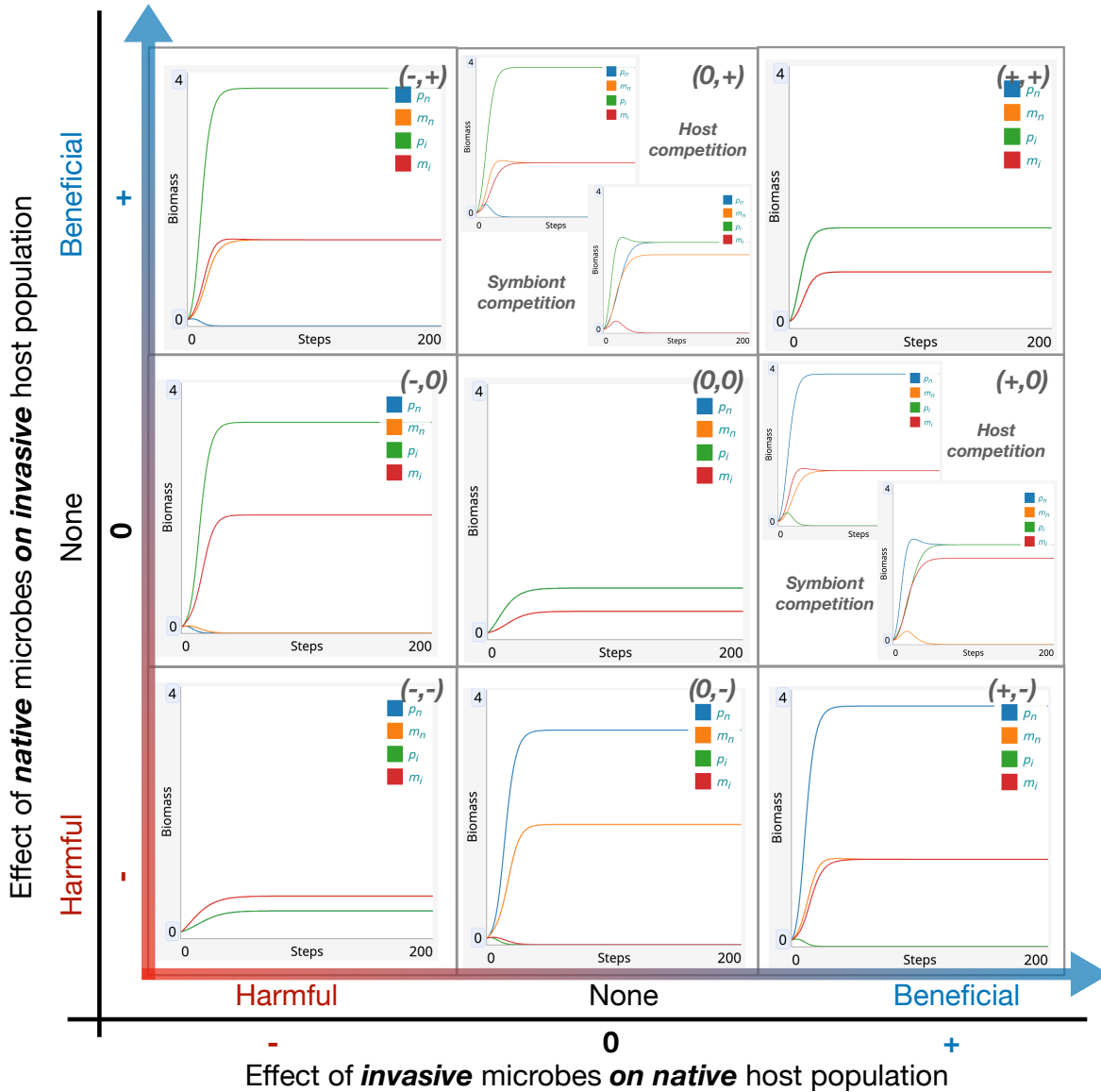


Fig. A.2: Timeseries produced by scenarios described in Fig. 3, for the parameter combinations provided in Table 1 and Table 1. Note that in scenarios (0, 0), (+, +) and (-, -) the curves representing native and invasive host biomass (p_n and p_i) and native and invasive microbial biomass (m_n and m_i) overlap. In this case, the coexistence steady state 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 I.1.4 and I.2.5. Scenarios (0, +) and (+, 0) are produced by assuming weak competition between hosts or symbionts, depending on whether we are looking at the symbiont or host competition scenario. In scenarios (-, +) and (+, -) we assume weak competition between symbionts.

920 B Analysis of the one host and one symbiont case

921 B.1 Steady state existence

922 **Obligate mutualist host** ($r_p = 0$): Consider the model of Eq. (1), consisting of only one
 923 host and its associated microbial community. We consider both host and symbiont to be
 924 obligate mutualists, i.e. $r_p = 0$. We obtain:

$$925 \begin{cases} \frac{dp}{dt} = \frac{pm}{\frac{p}{d} + m} \left(q_{hp} \frac{\alpha}{d} - q_{cp} \beta \right) - \mu_p p^2, \\ \frac{dm}{dt} = \frac{pm}{\frac{p}{d} + m} \left(q_{cm} \beta - q_{hm} \frac{\alpha}{d} \right) - \mu_m m^2. \end{cases} \quad (7)$$

We are interested in identifying the steady states of the system of Eq. (7) and their stability. For this purpose, we set $\frac{dp}{dt}$ and $\frac{dm}{dt}$ to zero and solve for p and m . Let us first define

$$\begin{cases} Q_p = q_{hp} \frac{\alpha}{d} - q_{cp} \beta, \\ Q_m = q_{cm} \beta - q_{hm} \frac{\alpha}{d}, \end{cases}$$

926 and consider

$$927 \begin{cases} \frac{dp}{dt} = 0 & \leftrightarrow & p = 0 & \text{or} & \frac{m}{\frac{p}{d} + m} Q_p - \mu_p p = 0, \\ \frac{dm}{dt} = 0 & \leftrightarrow & m = 0 & \text{or} & \frac{p}{\frac{p}{d} + m} Q_m - \mu_m m = 0. \end{cases} \quad (8)$$

928 Thus, a positive steady state state exists only for $Q_p, Q_m > 0$, i.e. for

$$929 \frac{q_{hp}}{q_{cp}} > \frac{\beta d}{\alpha} > \frac{q_{hm}}{q_{cm}}. \quad (9)$$

930 Note that if we choose to set $q_{cp} = q_{hm} = q_{cm} = 1$, and $\alpha = \beta$ (as chosen for simplicity in
 931 our simulations), in order for equation (9) to be satisfied, we need $q_{hp} > d$. Also note that for
 932 $d > 1$ (indicating that the host is larger than the symbiont), Eq. (9) implies that $Q_p > Q_m$.

933 For $Q_p > 0$ and $Q_m > 0$ we obtain the following nullclines for $p > 0$ and $m > 0$:

$$934 \begin{cases} p = 0 & \& m = \frac{\mu_p p^2}{d(Q_p - \mu_p p)} := n_1(p), \\ m = 0 & \& m = -\frac{p}{2d} + \frac{1}{2} \sqrt{\left(\frac{p}{d}\right)^2 + \frac{4pQ_m}{\mu_m}} := n_2(p). \end{cases} \quad (10)$$

935 Intersection of the nullclines $n_1(p)$ and $n_2(p)$ correspond to the steady state (p^*, m^*) . Note
 936 that $n_1(p)$ presents an asymptote at $p = \frac{Q_p}{\mu_p}$, meaning that $n_1(p) \rightarrow \infty$ for $p \rightarrow \frac{Q_p}{\mu_p}$. On the
 937 other hand, $n_2(p) \rightarrow \infty$ for $p \rightarrow \infty$.

938 Additionally, we know that the first derivative of $n_1(p)$ tends to zero at $p \rightarrow 0$ (i.e.,
 939 $n_1'(0) \rightarrow 0$), while $n_2'(0) > 0$. Thus, we conclude that a steady state (p^*, m^*) always exists,
 940 provided that $Q, Q' > 0$ (Eq. (9)). A graphical representation of the nullclines of Eq. (10) and
 941 their corresponding phase plane is plot in Fig. B.1a.

We can compute explicitly, the steady state (p^*, m^*) as follows.

$$\begin{aligned}
m^* &= -\frac{p^*}{2d} + \frac{1}{2} \sqrt{\left(\frac{p^*}{d}\right)^2 + \frac{4p^*Q_m}{\mu_m}} \\
m^* &= \frac{p^*}{\frac{p^*}{d} + m^*} \frac{Q_m}{\mu_m} \\
\frac{1}{\left(\frac{p^*}{d} + m^*\right)^2} Q_p Q_m - \mu_p \mu_m &= 0 \Rightarrow \frac{p^*}{d} + m^* = \sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}} \\
\Rightarrow \frac{p^*}{d} + \sqrt{\left(\frac{p^*}{d}\right)^2 + \frac{4p^*Q_m}{\mu_m}} &= 2 \sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}} \\
\Rightarrow p^* \left(\frac{Q_m}{\mu_m} + \frac{1}{d} \sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}} \right) &= \frac{Q_p Q_m}{\mu_m \mu_p}
\end{aligned}$$

We deduce that the steady state satisfies

$$p^* = \frac{\sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}}} \quad \text{and} \quad m^* = \frac{\frac{Q_m}{\mu_m}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}}}$$

942 **Facultative mutualist host** ($r_p > 0$): We can now look at the case in which the host is a
943 facultative mutualist, i.e., $r_p > 0$. The corresponding differential equation system is:

$$\begin{cases} \frac{dp}{dt} = r_p p + \frac{pm}{\frac{p}{d} + m} \left(q_{hp} \frac{\alpha}{d} - q_{cp} \beta \right) - \mu_p p^2, \\ \frac{dm}{dt} = \frac{pm}{\frac{p}{d} + m} \left(q_{cm} \beta - q_{hm} \frac{\alpha}{d} \right) - \mu_m m^2. \end{cases} \quad (11)$$

945 In this situation, host-symbiont coexistence may be observed as long as $Q_p + r_p > 0$, hence
946 as long as Q_p is larger than $-r_p$. Also for this case, we can compute the steady states, which
947 corresponds to the symbiont-free steady state $(p_0, 0)$, with $p_0 = r_p / \mu_p$, and the coexistence
948 steady state (p^*, m^*) , given by

$$p^* = p_0 + \frac{\frac{Q_p Q_m}{\mu_m \mu_p}}{\frac{S_1}{d} + \frac{Q_m}{\mu_m}} \quad \text{and} \quad m^* = \frac{d Q_m}{\mu_m} \frac{\frac{S_1}{d}}{\frac{S_1}{d} + \frac{Q_m}{\mu_m}} \quad (12)$$

where

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

950 The corresponding nullclines are shown in Fig. B.2.

951 Let us remark that if $Q_p > 0$, that is α large enough $\alpha \geq q_{cp} / q_{hp} \beta d$, the biomass of the
952 host in association with the symbiont is always larger than the biomass of the host alone

953 (p_0). Conversely, when $Q_p < 0$, that is $0 < \alpha \leq q_{cp}/q_{hp}\beta d$, the biomass of the host is reduced
 954 compared to its biomass alone. In this case we say that the symbiont is *parasitic* or *pathogenic*.

955 Moreover, we can show that the biomass of the host is not monotonic with the exchange
 956 rate α . It is increasing for $\alpha < \alpha^*$ such that $\partial_{\alpha} p^*(\alpha^*) = 0$ and decreasing for $\alpha \geq \alpha^*$ (see
 957 Fig. B.3).

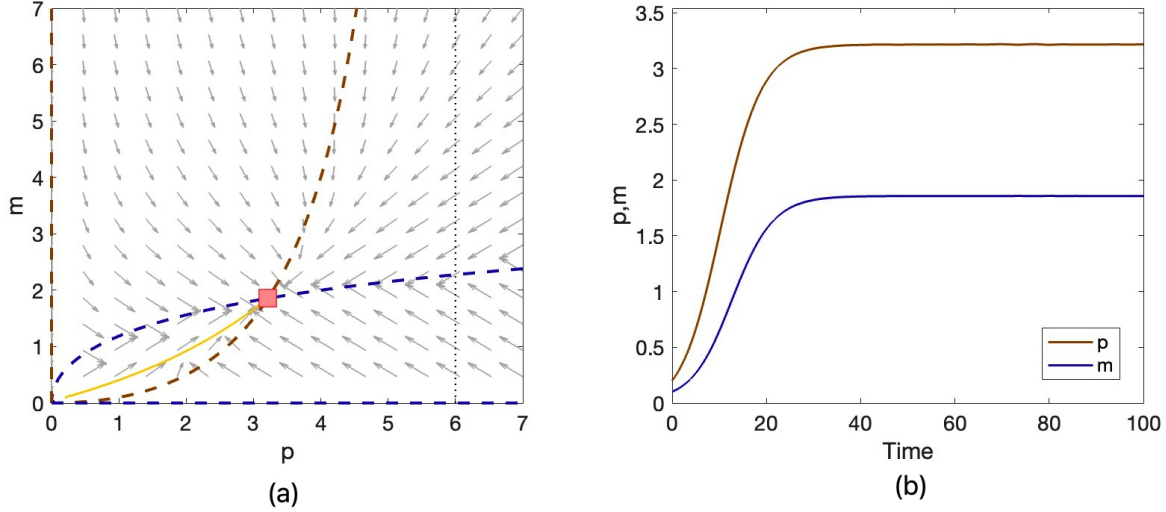


Fig. B.1: (a) Phase plane corresponding to the system of equations (7), for which $r_p = 0$. Brown dashed lines are nullclines found for $dp/dt = 0$, while blue dashed lines are nullclines found for $dm/dt = 0$. Intersection of the two non-zero nullclines corresponds to the stable steady state (p^*, m^*) , represented by the red square. The vertical black dotted line corresponds to the asymptote $p = Q_p/\mu_p$. (b) Temporal dynamics of p and m corresponding to the trajectory shown in orange in (a).

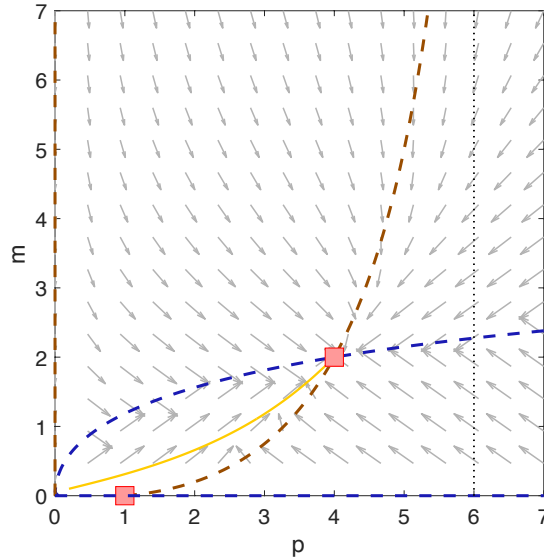


Fig. B.2: (a) Phase plane corresponding to the system of equations (11), for which $r_p > 0$. Brown dashed lines are nullclines found for $dp/dt = 0$, while blue dashed lines are nullclines found for $dm/dt = 0$. Intersection of the two non-zero nullclines corresponds to the stable steady state (p^*, 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 $p = Q_p/\mu_p$.

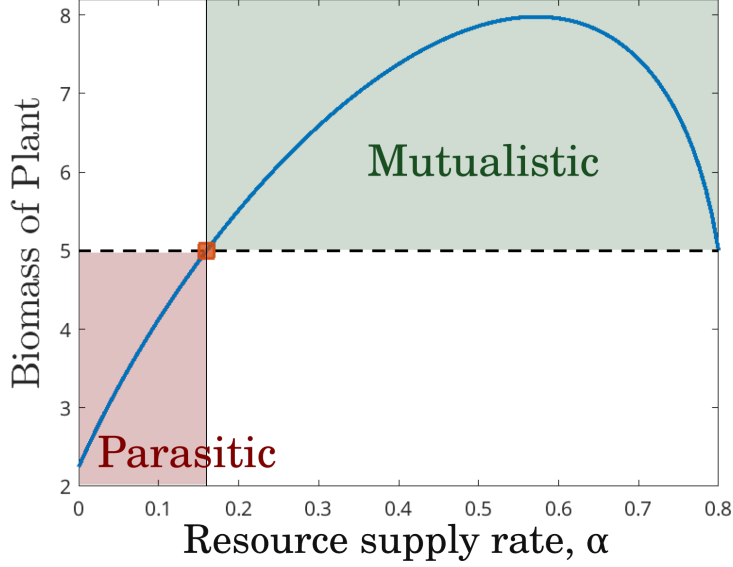


Fig. B.3: Parasitic or mutualistic symbiont. Evolution of the host biomass at equilibrium p^* defined by (12), with respect to the exchange rate α of the symbiont (blue plain curve). The host exchange rate β is fixed to $\beta = 0.4$. The dashed line corresponds to the biomass of the host alone $p_0 = r_p/\mu_p$. The red square corresponds to the critical value $\alpha = q_{cp}/q_{hp}\beta d$ (Eq. (9)).

958 B.2 Steady state stability

959 **Obligate mutualist host** ($r_p = 0$): To derive the stability of the steady state (p^*, m^*) , we
 960 compute the Jacobian of the system of equation (7). We obtain:

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

961 From Eq. (8), we know that at steady state

$$962 \begin{cases} \frac{m^*}{\frac{p^*}{d} + m^*} Q_p = \mu_p p^* \\ \frac{p^*}{\frac{p^*}{d} + m^*} Q_m = \mu_m m^*. \end{cases} \quad (13)$$

Thus the Jacobian J can be written as

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

We can see right away that $\text{Tr}(J) < 0$. To prove stability of (p^*, m^*) we should therefore only show that $\text{Det}J > 0$. We have

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

963 Therefore, we showed that a unique stable steady (p^*, m^*) always exists for $Q_p, Q_m > 0$. The
964 temporal dynamics of p and m over time is shown in Fig. B.1b.

965 **Facultative mutualist host** ($r_p > 0$): To derive the stability of the steady state (p^*, m^*)
966 for the case where $r_p > 0$ we compute the Jacobian of the system of equation (11). We obtain:

$$967 \quad J(p^*, m^*) = \frac{1}{\frac{p^*}{d} + m^*} \begin{pmatrix} \frac{m^{*2}}{\frac{p^*}{d} + m^*} Q_p + (r_p - 2\mu_p p^*) \left(\frac{p^*}{d} + m^* \right) & \frac{p^{*2}}{\left(\frac{p^*}{d} + m^* \right)} Q_p \\ \frac{m^{*2}}{\left(\frac{p^*}{d} + m^* \right)} Q_m & \frac{p^{*2}}{\frac{p^*}{d} + m^*} Q_m - 2\mu_m m^* \left(\frac{p^*}{d} + m^* \right) \end{pmatrix}. \quad (14)$$

968 From Eq. (8), we know that at steady state

$$969 \quad \begin{cases} \frac{m^*}{\frac{p^*}{d} + m^*} Q_p = \mu_p p^* - r_p = \mu_p (p^* - p_0) \\ \frac{p^*}{\frac{p^*}{d} + m^*} Q_m = \mu_m m^*. \end{cases} \quad (15)$$

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 $q_{hp}q_{cm}/(q_{cp}q_{hm}) > 1$. 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

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

970 Therefore, we showed that the unique positive stable steady state (p^*, m^*) always exists for
 971 $r_p \geq 0$, $Q_m > 0$ and $Q_p \geq -r_p$. The temporal dynamics of p and m over time is shown in
 972 Fig. B.1b.

973 **C Analysis of the one host and multiple symbionts case** 974 **(no competition)**

Consider the function f_m , proportional to the rate at which a symbiont provides a resource to the host:

$$f_m = m \frac{p}{p + md}, \text{ i.e., } f_m = \begin{cases} m & \text{if } p \gg md, \\ \frac{p}{d} & \text{if } p \ll md. \end{cases}$$

Similarly, the rate at which a host provides resources to a symbiont, depends on:

$$f_p = p \frac{m}{m + \frac{p}{d}}, \text{ i.e., } f_p = \begin{cases} p & \text{if } m \gg \frac{p}{d}, \\ md & \text{if } m \ll \frac{p}{d}. \end{cases}$$

In the presence of multiple microbial communities, dm needs to be substituted by $d \sum_i m_i$, for $i = 1, \dots, N$ such that the rate at which each symbiont provides resource to the host is proportional to:

$$f_{m_i} = m_i \frac{p}{p + \sum_i m_i d}, \text{ i.e., } f_{m_i} = \begin{cases} m_i & \text{if } p \gg \sum_i m_i d, \\ \frac{m_i}{\sum_i m_i} \frac{p}{d} & \text{if } p \ll \sum_i m_i d, \end{cases}$$

and the rate at which the host provides nutrients to symbiont i is proportional to

$$f_p = p \frac{m_i}{\sum_i m_i + \frac{p}{d}}, \text{ i.e., } f_p = \begin{cases} p \frac{m_i}{\sum_i m_i} & \text{if } \sum_i m_i \gg \frac{p}{d}, \\ m_i d & \text{if } \sum_i m_i \ll \frac{p}{d}. \end{cases}$$

975 Thus, we obtain:

$$\begin{cases} \frac{dp}{dt} = r_p + \frac{p}{\frac{p}{d} + \sum_i m_i} \sum_i m_i Q_{p_i} - \mu_p p^2, \\ \frac{dm_i}{dt} = \frac{p m_i}{\frac{p}{d} + \sum_i m_i} Q_{m_i} - \mu_m m^2, \quad \text{for } i = 1, \dots, N. \end{cases} \quad (16)$$

977 **C.1 Steady state existence**

The host, that might be obligate or facultative mutualists ($r_p \geq 0$), and symbionts exchange with it at rates given by

$$Q_{p_i} = q_{hp} \frac{\alpha_i}{d} - q_{cp} \beta_i \quad \text{and} \quad Q_{m_i} = q_{cm} \beta_i - q_{hm} \frac{\alpha_i}{d}.$$

To compute the steady state, let us define the three following vectors \mathbf{Q}_p , \mathbf{Q}_m and \mathbf{p}_0

$$\mathbf{Q}_m = \begin{pmatrix} Q_{m_1} \\ \vdots \\ Q_{m_N} \end{pmatrix} \text{ and } \mathbf{Q}_p = (Q_{p_1} \ \cdots \ Q_{p_N}) \text{ and } p_0 = \frac{r_p}{\mu_p},$$

978 and let us denote $S = \frac{p}{d} + \sum_{i=1}^N m_i$.

979 A steady state (p, m_1, \dots, m_N) , that we write (p, \mathbf{m}) with $\mathbf{m} = (m_1, \dots, m_N)$, will satisfy
980 the following problem

$$981 \quad \frac{1}{S} \mathbf{Q}_p \mathbf{m} = \mu_p p - \mu_{p_0} \text{ and } \frac{1}{S} \mathbf{Q}_m p = \mu_m \mathbf{m}. \quad (17)$$

982 Combining the two systems, we obtain

$$983 \quad \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_m \mu_p} \mathbf{m} = S^2 \mathbf{m} - S \frac{\mathbf{Q}_m}{\mu_m} p_0 \text{ and } \frac{\mathbf{Q}_p \mathbf{Q}_m}{\mu_p \mu_m} p = S^2 (p - p_0)$$

. We can reformulate the system as follows

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

984 where $\mathbf{A} = \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_m \mu_p}$ and $\mathbf{q}_0 = \mathbf{Q}_m / \mu_m p_0$.

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

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

We can compute \mathbf{m} as follow:

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

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

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

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

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

So we can deduce that S is given by

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

Finally, we get

$$p = p_0 + \frac{\frac{\mathbf{Q}_p\mathbf{Q}_m}{\mu_p\mu_m}}{\frac{S}{d} + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m}} \quad \text{and} \quad \mathbf{m} = \frac{S}{\frac{S}{d} + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m}} \frac{\mathbf{Q}_m}{\mu_m}.$$

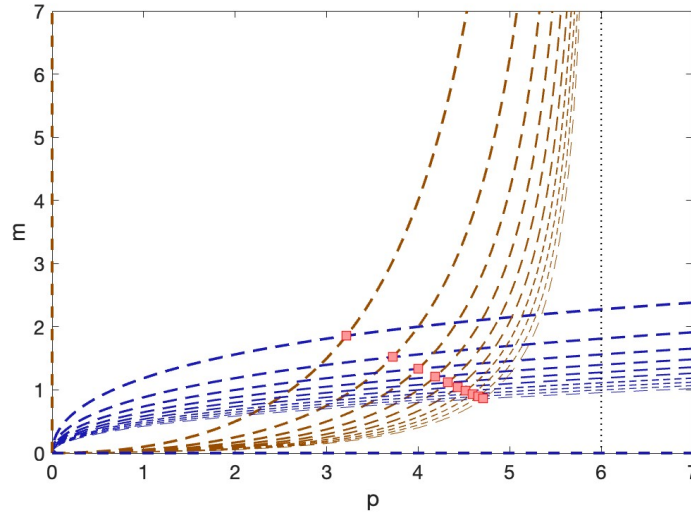


Fig. C.1: Nullclines of the system of Eq. (16), when considering that all symbionts are identical. Curves represent the nullclines for $N = 1$ (thicker line) till $N = 10$ (thinner line). The corresponding steady states for different values of N are indicated by the red squares. Note that for N large, m^* decreases while p^* increases.

985 **Case of N similar symbionts** We here assume that exchange rates are similar among the
 986 symbionts community, that is $\alpha_i = \alpha$ and $\beta_i = \beta$ for all $i \in \{1, \dots, N\}$. In this case, the
 987 biomass of symbiont at equilibrium are all equal to m^* and the steady state (p^*, \mathbf{m}^*) can be
 988 expressed as

$$989 \quad p^* = p_0 + \frac{\frac{\mathbf{Q}_p\mathbf{Q}_m}{\mu_p\mu_m}}{\frac{S_N}{\sqrt{N}d} + \frac{\mathbf{Q}_m}{\mu_m}} \quad \text{and} \quad m^* = \frac{d\mathbf{Q}_m}{\mu_m} \frac{\frac{S_N}{d\sqrt{N}}}{\frac{S_N}{d\sqrt{N}} + \frac{\mathbf{Q}_m}{\mu_m}}, \quad (18)$$

where

$$S_N = \frac{p_0}{2\sqrt{N}d} + \sqrt{\frac{1}{N} \left(\frac{p_0}{2d}\right)^2 + \frac{\mathbf{Q}_m}{\mu_m}p_0 + \frac{\mathbf{Q}_m\mathbf{Q}_p}{\mu_m\mu_p}}.$$

990 C.2 Steady state stability with similar species

991 To gain insights into conditions for the existence of a stable steady state of coexistence of a
 992 host and multiple microbes, we compute the $(N \times N)$ -Jacobian of the system of Eq. (16) at
 993 (p^*, m^*, \dots, m^*) . The corresponding Jacobian is:

$$994 \quad J = \begin{pmatrix} j_p & b & \cdots & \cdots & b \\ c & j_m & e & \cdots & e \\ \vdots & e & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & e \\ c & e & \cdots & e & j_m \end{pmatrix}, \text{ where } \begin{cases} j_p = -\frac{p^* m^* N Q_p}{d \left(\frac{p}{d} + N m^*\right)^2} - \mu_p p^* < 0 \\ b = \frac{(p^*)^2 Q_p}{d \left(\frac{p}{d} + N m^*\right)^2} > 0 \\ c = \frac{N (m^*)^2 Q_m}{\left(\frac{p}{d} + N m^*\right)^2} > 0 \\ j_m = -\frac{p^* m^* Q_m}{\left(\frac{p}{d} + N m^*\right)^2} - \mu_m m^* < 0 \\ e = -\frac{p^* m^* Q_m}{\left(\frac{p}{d} + N m^*\right)^2} - c m^* = j_m + \mu_m m^* < 0 \end{cases} \quad (19)$$

We observe that $j_m - e = -\mu_m m^*$ is an eigenvalue of multiplicity $N - 1$ of J associated to the eigenvectors \mathbf{v}_i for $i \in \{2, \dots, N\}$, where $\mathbf{v}_i(i) = -\mathbf{v}_i(i+1) = 1$ and $\mathbf{v}_i(j) = 0$ for $j \neq i$ and $i \in \{2, \dots, N\}$. Thus, the characteristic polynomial of J can be factorized as follows:

$$\det(J - \lambda I) = (\lambda + \mu_m m^*)^{N-1} (\lambda^2 + A\lambda + B),$$

where

$$A = -\text{Tr}(J) + (N-1)(j_m - e) = -j_p - j_m - e(N-1) > 0 \quad \text{and} \\ B = \frac{(-1)^{N+1} \det(J)}{-(j_m - e)^{N-1}} = j_p(j_m + e(N-1)) - 2bc > 0.$$

995 The coefficient A and B are positive, so the eigenvalues of the Jacobian are all negative.

996 C.3 Harmful and beneficial microbes

997 As explained in the main text, our definition of ‘harmful’ or ‘beneficial’ microbes depends on
 998 whether host biomass at equilibrium decreases or increases after the addition of the symbiont.
 999 Host biomass depends on all model parameters, as shown in the SI B, and on the number of
 1000 symbionts (see e.g. Eq. (18)).

1001 Let us consider the situation in which a symbiont is added to a host-symbiont pair, e.g., a
 1002 native host, associated with its microbes. Let us assume that native and invasive symbionts
 1003 differ by the rate at which resources are transferred to the host, e.g., by parameter α_{in} and
 1004 α_{nn} and to the symbiont, e.g., by parameter β_{nn} and β_{ni} . We keep α_{nn} fix to 0.4, and vary
 1005 α_{in} and compute the steady state $p_n^*(\alpha_{nn}, \alpha_{in})$ for different values of α_{in} . Results are shown
 1006 in Fig. C.3.

Obligate mutualist host ($r_p = 0$) In this case, we can compute the coexistence steady state $(p_n^*(\alpha_{nn}, \alpha_{in}), m_n^*, m_i^*)$, as follows. Let us define the exchange rates

$$\begin{cases} Q_p &= q_{hp} \frac{\alpha_{nn}}{d} - q_{cp} \beta_{nn}, \\ Q_m &= q_{cm} \beta_{nn} - q_{hm} \frac{\alpha_{nn}}{d}, \end{cases} \quad \text{and} \quad \begin{cases} q_p &= q_{hp} \frac{\alpha_{in}}{d} - q_{cp} \beta_{ni} = Q_p + q_{hp} \frac{\alpha_{in} - \alpha_{nn}}{d}, \\ q_m &= q_{cm} \beta_{ni} - q_{hm} \frac{\alpha_{in}}{d} = Q_m - q_{hm} \frac{\alpha_{in} - \alpha_{nn}}{d}, \end{cases}$$

1007 where Q_p and Q_m are exchanges between the native host and its native symbiont, while
 1008 q_p, q_m are the exchange rates between the native host and the invasive symbiont. If $q_m \geq 0$,
 1009 we obtain that the biomass at coexistence equilibrium is given by the following formula

$$1010 \quad p_n^*(\alpha_{nn}, \alpha_{in}) = \frac{\sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}} \sqrt{1 + \frac{q_p q_m}{Q_p Q_m}}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}} \frac{1 + \frac{q_m}{Q_m}}{\sqrt{1 + \frac{q_p q_m}{Q_p Q_m}}}} = p_n^*(\alpha_{nn}, 0) \frac{\left(\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}}\right) \sqrt{1 + \frac{q_p q_m}{Q_p Q_m}}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}} \frac{1 + \frac{q_m}{Q_m}}{\sqrt{1 + \frac{q_p q_m}{Q_p Q_m}}}},$$

1011 where $p_n^*(\alpha_{nn}, 0)$ is the biomass of the native host at equilibrium only with its native symbiont:

$$1012 \quad p_n^*(\alpha_{nn}, 0) = \frac{\sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}}}.$$

1013 One can observe that if the invasive symbiont is too parasitic for the native host, that
 1014 is $q_p \leq -\frac{Q_p Q_m}{q_m}$, which corresponds to very small value of α_{in} (see dashed in Fig.C.3), the
 1015 coexistence steady state does not exist. In addition, if the symbiont is parasitic, that is $q_p < 0$,
 1016 which corresponds to $\alpha_{in} \leq q_{cp} \beta_{ni} d / q_{hp}$, then $p_n^*(\alpha_{in}, \alpha_{nn}) < p_n^*(0, \alpha_{nn})$, which implies that
 1017 the critical threshold α_{in}^* such that $p_n^*(\alpha_{in}^*, \alpha_{nn}) = p_n^*(0, \alpha_{nn})$ satisfies

$$1018 \quad \alpha_{in}^* > \frac{q_{cp}}{q_{hp}} \beta_{ni} d.$$

1019 It means that also symbionts that provide some benefit to their host can be parasitic or
 1020 pathogenic, if their mutualistic investment α_{in} is lower than α_{in}^* .

When the exchange rate to symbionts are identical $\beta_{ni} = \beta_{nn}$, we can show that if the
 invasive symbiont is as beneficial as the native symbiont (i.e., $\alpha_{in} = \alpha_{nn}$), then $p_n^*(\alpha_{nn}, \alpha_{nn}) >$
 $p_n^*(0, \alpha_{nn})$. Thus the critical threshold α_{in}^* such that $p_n^*(\alpha_{in}^*, \alpha_{nn}) = p_n^*(0, \alpha_{nn})$ satisfies

$$\frac{q_{cp}}{q_{hp}} \beta_{ni} d < \alpha_{in}^* < \alpha_{nn}.$$

1021 Finally, if the invasive symbiont is too mutualistic, that is α_{in} is very large such that
 1022 $\alpha_{in} \rightarrow \frac{q_{cm}}{q_{hm}} \beta d$ (which corresponds to the case where the exchange rate $q_m \rightarrow 0$), the symbiont
 1023 can not grow. In this case, we obtain that $p_n^*(\alpha_{in}^*, \alpha_{nn}) \rightarrow p_n^*(0, \alpha_{nn})$ as $q_m \rightarrow 0$, and we
 1024 observe that the biomass of the host in association with the two symbionts tends to be
 1025 identical as its biomass only with its native symbionts. The coexistence state exists only
 1026 if $q_m \geq 0$. Otherwise, exclusion occurs.

1027 **Facultative mutualist host** ($r_p > 0$) In this case, we define $p_0 = r_p / \mu_p$, as the carrying ca-
 1028 pacity of the host alone, and we can compute the coexistence steady state ($p_n^*(\alpha_{nn}, \alpha_{in}), m_n^*, m_i^*$)
 1029 as follows:

$$1030 \quad p_n^*(\alpha_{nn}, \alpha_{in}) = p_0 + \frac{\frac{Q_p Q_m}{\mu_m \mu_p} \left(1 + \frac{q_p q_m}{Q_p Q_m}\right)}{\frac{S_{ni}}{d} + \frac{Q_m}{\mu_m} \left(1 + \frac{q_m}{Q_m}\right)},$$

1031 where S_{ni} is given by

$$1032 \quad S_{ni} = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d}\right)^2 + p_0 \frac{Q_m}{\mu_m} \left(1 + \frac{q_m}{Q_m}\right) + \frac{Q_m Q_p}{\mu_m \mu_p} \left(1 + \frac{q_m q_p}{Q_m Q_p}\right)}.$$

1033 In absence of the invasive symbionts, we have the following expression $p_n^*(\alpha_{nn}, 0)$ of the biomass
1034 of the native host at equilibrium only with its native symbiont:

$$1035 \quad p_n^*(\alpha_{nn}, 0) = p_0 + \frac{\frac{Q_p Q_m}{\mu_m \mu_p}}{\frac{S_n}{d} + \frac{Q_m}{\mu_m}},$$

1036 where S_n is given by

$$1037 \quad S_n = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d}\right)^2 + p_0 \frac{Q_m}{\mu_m} + \frac{Q_m Q_p}{\mu_m \mu_p}}.$$

1038 The critical value α_{in}^* such that $p_n^*(\alpha_{nn}, 0) = p_n^*(\alpha_{nn}, \alpha_{in}^*)$ can be approximated by the
1039 following formula

$$1040 \quad \alpha_{in}^* \approx \frac{q_{cp}}{q_{hp}} \beta_{ni} d + \frac{d}{q_{hp}} \frac{\frac{Q_m Q_p}{\mu_m} S_n}{\left(\frac{S_n}{d} + \frac{Q_m}{\mu_m}\right) \sqrt{\left(\frac{p_0}{2d}\right)^2 + p_0 \frac{Q_m}{\mu_m} + \frac{Q_m Q_p}{\mu_m \mu_p}} - \frac{1}{2d} \frac{Q_m Q_p}{\mu_m \mu_p}}. \quad (20)$$

1041 In the particular when $\beta_{nn} = \beta_{ni} = \beta$, the critical value α_{in}^* satisfies

$$1042 \quad \alpha_{in}^* \approx \alpha_{nn} - \frac{d}{q_{hp}} \left(Q_p - \frac{\frac{Q_m Q_p}{\mu_m} S_n}{\left(\frac{S_n}{d} + \frac{Q_m}{\mu_m}\right) \sqrt{\left(\frac{p_0}{2d}\right)^2 + p_0 \frac{Q_m}{\mu_m} + \frac{Q_m Q_p}{\mu_m \mu_p}} - \frac{1}{2d} \frac{Q_m Q_p}{\mu_m \mu_p}} \right). \quad (21)$$

1043 In Fig. C.3(a)-(b) we consider that the host is an obligate mutualist ($r_p = 0$), while
1044 in Fig. C.3(b) the host is a facultative mutualist. Increasing α_{ni} increases host biomass at
1045 equilibrium p_i^* . We can see that $p_i^*(m_n(\alpha_{ni}), m_i(\alpha_{ii})) > p_i^*(0, m_i(\alpha_{ii}))$ for α_{in} large enough,
1046 meaning that the biomass at equilibrium of a host associated with two symbionts characterized
1047 by the same α is larger than the biomass of the same host associated with only one symbiont.
1048 Further increasing the value of α_{ni} decreases the ability of the symbiont m_n to grow, and to
1049 supply resource to the host. Thus, $p_i^*(m_n(\alpha_{ni}), m_i(\alpha_{ii})) = p_i^*(0, m_i(\alpha_{ii}))$ for α_{ni} large enough.

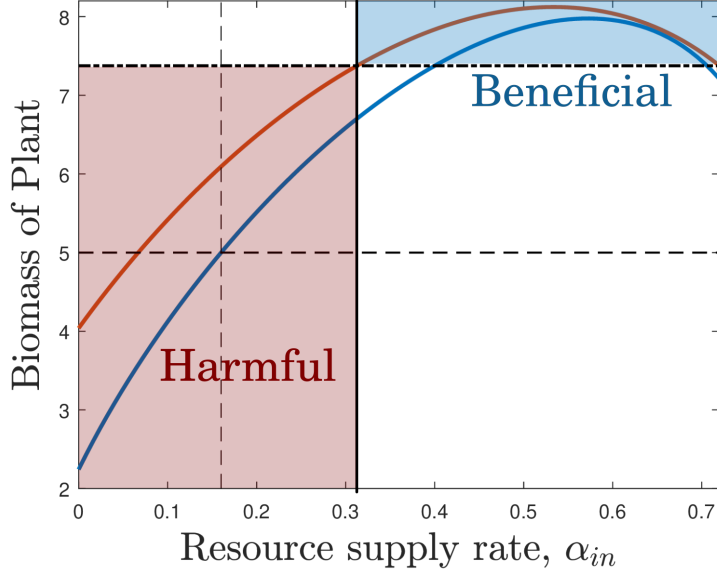


Fig. C.2: Host biomass at equilibrium when the host is considered in association with one symbiont (blue curve), characterized by the resource supply rate α_{in} , or with two symbionts (red curve), where one symbiont is characterised by the resource supply rate $\alpha_{nn} = 0.4$, while the other is characterised by resource supply rate α_{in} . The black dash-dotted line corresponds to the biomass of the host in association only with one native with constant resource exchange parameter $\alpha_{nn} = 0.4$. The dashed line corresponds to the biomass of the host in the absence of symbionts (with $r_p = 0.5$). The black plain vertical line corresponds to the critical value of the resource exchange rate α_{in}^* below which the addition of an introduced symbiont (when a beneficial native symbiont is already present) is considered harmful. The dashed vertical line the minimal value of the resource exchange parameter α required by a symbiont in order to be mutualistic for the host, when no other symbionts are present.

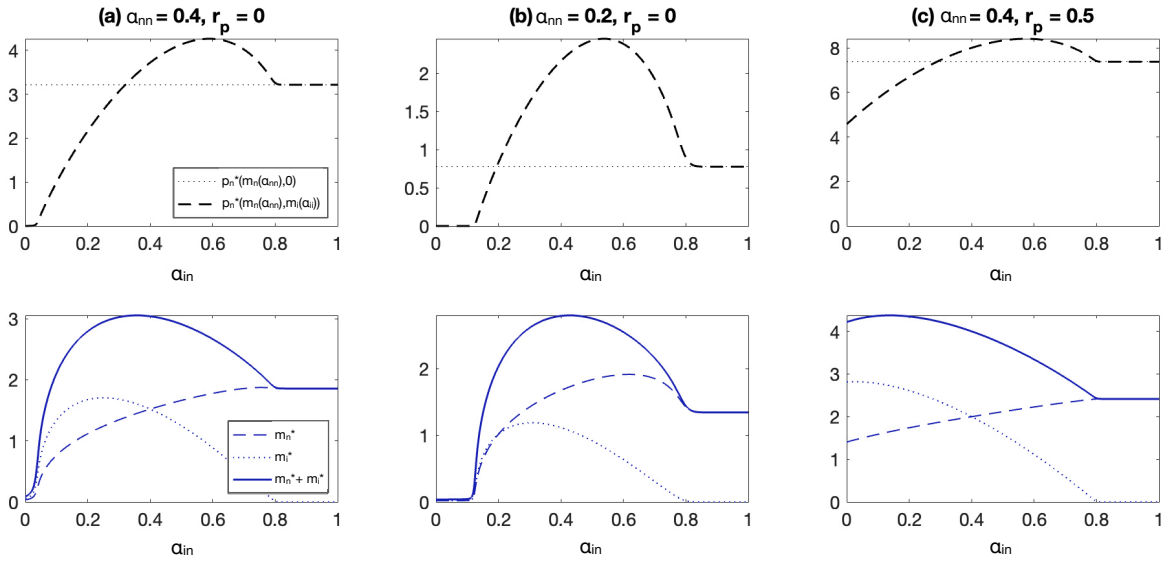


Fig. C.3: Host (upper figures) and symbiont biomasses (lower figures) at equilibrium when the host is considered in association with two symbionts characterized by resource supply rates α_{ii} and α_{ni} respectively. Parameter α_{ii} is kept constant at 0.4 (in (a) and (c)), or 0.2 (in (b)), while α_{ni} is varied from 0 to 1. In (a) and (b) the host is an obligate mutualist, and $r_p = 0$. In (c), the host is a facultative mutualist, and $r_p = 0.5$.

D Analysis of the one symbiont and multiple hosts case (no competition)

Consider now the situation in which we have one symbiont and multiple hosts. In the presence of multiple hosts, p/d needs to be substituted by $\sum_j p_j/d$, for $j = 1, \dots, N$ such that the rate at which a symbiont provides resources to host j is proportional to:

$$f_m = m \frac{p_j}{\sum_j p_j + md}, \text{ i.e., } f_m = \begin{cases} m \frac{p_j}{\sum_j p_j} & \text{if } \sum_j p_j \gg md, \\ \frac{p_j}{d} & \text{if } \sum_j p_j \ll md, \end{cases}$$

and the rate at which each host provides resources to its symbionts is proportional to

$$f_{p_j} = p_j \frac{m_i}{m_i + \frac{\sum_j p_j}{d}}, \text{ i.e., } f_{p_j} = \begin{cases} p_j & \text{if } m \gg \frac{\sum_j p_j}{d}, \\ \frac{p_j}{\sum_j p_j} md & \text{if } m \ll \frac{\sum_j p_j}{d}. \end{cases}$$

Thus, we obtain:

$$\begin{cases} \frac{dp_j}{dt} = r_{p_i} p_i + \frac{p_j}{\frac{\sum_j p_j}{d} + m} m Q_{p_j} - \mu_p p_j^2 & \text{for } i = 1, \dots, N, \\ \frac{dm}{dt} = \frac{m}{\frac{\sum_j p_j}{d} + m} \sum_j p_j Q_{m_j} - \mu_m m^2. \end{cases} \quad (22)$$

Steady state with one symbiont and multiple hosts

The hosts might be obligate or facultative mutualists ($r_{p_i} \geq 0$, $i \in \{1, \dots, N\}$) and a symbiont exchanges with both hosts at rates given by

$$Q_{p_i} = q_{hp} \frac{\alpha_i}{d} - q_{cp} \beta_i \quad \text{and} \quad Q_{m_i} = q_{cm} \beta_i - q_{hm} \frac{\alpha_i}{d}.$$

To compute the steady state, let us define the three following vectors \mathbf{Q}_p , \mathbf{Q}_m and \mathbf{p}_0 :

$$\mathbf{Q}_p = \begin{pmatrix} Q_{p_1} \\ \vdots \\ Q_{p_2} \end{pmatrix} \quad \text{and} \quad \mathbf{Q}_m = (Q_{m_1} \quad \cdots \quad Q_{m_2}) \quad \text{and} \quad \mathbf{p}_0 = \frac{1}{\mu_p} \begin{pmatrix} r_{p_1} \\ \vdots \\ r_{p_2} \end{pmatrix},$$

and let us denote $S = \frac{1}{d} \sum_{i=1}^N p_i + m$.

A steady state (p_1, \dots, p_N, m) , that we write (\mathbf{p}, m) with $\mathbf{p} = (p_1, \dots, p_N)$, will satisfy the following problem:

$$\frac{1}{S} \mathbf{Q}_p m = \mu_p \mathbf{p} - \mu_p \mathbf{p}_0 \quad \text{and} \quad \frac{1}{S} \mathbf{Q}_m \mathbf{p} = \mu_m m. \quad (23)$$

Combining the two systems, we obtain:

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

We can reformulate the system as follows:

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

1061 where $\mathbf{A} = \frac{\mathbf{Q}_p \mathbf{Q}_m}{\mu_p \mu_m}$, and $q_0 = \frac{\mathbf{Q}_m}{\mu_m} \mathbf{p}_0$.

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

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

We can compute \mathbf{p} as follow

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

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

$$\begin{aligned} S &= \frac{1}{d} \mathbf{e} \mathbf{p} + m \\ &= \frac{1}{d} \frac{S^2 \mathbf{e} \mathbf{p}_0}{S^2 - \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_p \mu_m}} + \frac{1}{d} \frac{\mathbf{e} \left(\mathbf{A} - \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_p \mu_m} \right) \mathbf{p}_0}{S^2 - \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_p \mu_m}} + \frac{S q_0}{S^2 - \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_p \mu_m}}, \end{aligned}$$

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

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

1062 **E Analysis of the multiple symbionts and multiple hosts** 1063 **case (no competition)**

The rate at which each symbiont i supplies a resource to each host j is proportional to

$$f_{m_i} = m_i \frac{p_j}{\sum_j p_j + \sum_i m_i d}, \text{ i.e., } f_{m_i} = \begin{cases} m_i \frac{p_j}{\sum_j p_j} & \text{if } \sum_j p_j \gg \sum_i m_i d, \\ \frac{p_j}{d} \frac{m_i}{\sum_i m_i} & \text{if } \sum_j p_j \ll \sum_i m_i d, \end{cases}$$

and the rate at which each host j provides resources to a symbiont i is proportional to

$$f_{p_j} = p_j \frac{m_i}{\sum_i m_i + \frac{\sum_j p_j}{d}}, \text{ i.e., } f_{p_j} = \begin{cases} p_j \frac{m_i}{\sum_i m_i} & \text{if } \sum_i m_i \gg \frac{\sum_j p_j}{d}, \\ \frac{p_j}{\sum_j p_j} m_i d & \text{if } \sum_i m_i \ll \frac{\sum_j p_j}{d}. \end{cases}$$

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Thus, we obtain the following system with M hosts and N symbionts

$$\begin{cases} \frac{dp_j}{dt} = \frac{p_j}{\frac{d}{\sum_j p_j} + \sum_i m_i} \sum_i m_i Q_{p_{ij}} - \mu_p p_j^2, & \text{for } j = 1, \dots, M, \\ \frac{dm_i}{dt} = \frac{m_i}{\frac{d}{\sum_j p_j} + \sum_i m_i} \sum_j p_j Q_{m_{ji}} - \mu_m m_i^2, & \text{for } i = 1, \dots, N, \end{cases} \quad (24)$$

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where $Q_{p_{ij}}$ is the effect of AMF i on host j and $Q_{m_{ji}}$ is the effect of host j on AMF i . They are defined for any $i, j \in \{1, 2\}$ by

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

To compute the steady state, let us define the two following matrices \mathbf{Q}_p and \mathbf{Q}_m

$$\mathbf{Q}_p = \begin{pmatrix} Q_{p_{11}} & \cdots & Q_{p_{1N}} \\ \vdots & & \vdots \\ Q_{p_{M1}} & \cdots & Q_{p_{MN}} \end{pmatrix} \quad \text{and} \quad \mathbf{Q}_m = \begin{pmatrix} Q_{m_{11}} & \cdots & Q_{m_{1M}} \\ \vdots & & \vdots \\ Q_{m_{N1}} & \cdots & Q_{m_{NM}} \end{pmatrix},$$

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and let us denote $S = \frac{1}{d} \sum_{i=1}^M p_i + \sum_{j=1}^N m_j$.

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E.1 Coexistence steady state with obligate hosts ($r_{p_i} = 0$)

A steady state $(p_1, \dots, p_M, m_1, \dots, m_N) = (\mathbf{p}, \mathbf{m})$, with $\mathbf{p} = (p_1, \dots, p_M)$ and $\mathbf{m} = (m_1, \dots, m_N)$ will satisfy the following system

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

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Combining the two systems we show that, if it exists, S^2 is the positive eigenvalue of the matrix $\mathbf{Q}_m \mathbf{Q}_p / \mu_m \mu_p$ and \mathbf{m} is its associated positive eigenvector, while \mathbf{p} is the positive eigenvector associated to matrix $\mathbf{Q}_p \mathbf{Q}_m / \mu_p \mu_m$ with the same eigenvalue. If the matrices are positive, their eigenpair exists thanks to Perron-Frobenius theorem and it satisfies the following system

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$$\frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_m \mu_p} \mathbf{m} = S^2 \mathbf{m} \quad \text{and} \quad \frac{\mathbf{Q}_p \mathbf{Q}_m}{\mu_p \mu_m} \mathbf{p} = S^2 \mathbf{p}.$$

In particular, the eigenpair is unique if the matrix $\mathbf{Q}_m \mathbf{Q}_p / \mu_m \mu_p$ is primitive. Nevertheless, the eigenvectors are unique up to a scalar factor. Let us define \mathbf{x}_p and \mathbf{x}_m , the normalized eigenvector associated to S^2 that satisfies $\sum_{i=1}^M x_{p_i} = \sum_{j=1}^N x_{m_j} = 1$. Then $\mathbf{p} = P \mathbf{x}_p$ and $\mathbf{m} = M \mathbf{x}_m$, where P and M are respectively the total biomass of hosts and symbionts. These quantities satisfy

$$P = \frac{S^2}{\frac{d}{S} + \frac{\mathbf{e} \mathbf{Q}_m \mathbf{x}_p}{\mu_m}} \quad \text{and} \quad M = \frac{S \frac{\mathbf{e} \mathbf{Q}_m \mathbf{x}_p}{\mu_m}}{\frac{d}{S} + \frac{\mathbf{e} \mathbf{Q}_m \mathbf{x}_p}{\mu_m}}.$$

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Case of two hosts and two symbionts ($N = M = 2$) In this case we can compute the value of S^2 by finding the positive root of the characteristic polynomial of the matrix, that is

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$$S^2 = \frac{\text{Tr}(\mathbf{Q}_m \mathbf{Q}_p)}{2\mu_m \mu_p} + \frac{1}{2} \sqrt{\left(\frac{\text{Tr}(\mathbf{Q}_m \mathbf{Q}_p)}{\mu_m \mu_p} \right)^2 - 4 \frac{\det(\mathbf{Q}_m \mathbf{Q}_p)}{(\mu_m \mu_p)^2}}.$$

1076 In scenarios $(0, +)$, $(+, +)$ and $(+, 0)$, the matrices $\mathbf{Q}_m \mathbf{Q}_p$ and $\mathbf{Q}_p \mathbf{Q}_m$ are positive and thus
 1077 primitive. As consequences, the positive steady state always exists in this situation as well as
 1078 the exclusion steady state.

1079 The coexistence steady state exist for the scenario $(0, 0)$, because the matrices \mathbf{Q}_m and
 1080 \mathbf{Q}_p are proportional to the identity matrix. However, for the scenario $(0, -)$ or $(-, 0)$, the
 1081 discriminant is negative and there is no positive eigenpair, meaning that exclusion occurs. In
 1082 the extreme scenarios $(-, -)$, $(+, -)$ or $(-, +)$, coexistence may occur.

1083 Moreover, we can explicitly compute the steady state as follow:

$$\begin{aligned}
 P &= \frac{S}{\frac{1}{d} + \frac{Q_{m11} + Q_{m21}}{\mu_m} \frac{x_1}{S} + \frac{Q_{m12} + Q_{m22}}{\mu_m} \frac{x_2}{S}} \quad \text{and} \quad M = \frac{\frac{Q_{m11} + Q_{m21}}{\mu_m} x_1 + \frac{Q_{m12} + Q_{m22}}{\mu_m} x_2}{\frac{1}{d} + \frac{Q_{m11} + Q_{m21}}{\mu_m} \frac{x_1}{S} + \frac{Q_{m12} + Q_{m22}}{\mu_m} \frac{x_2}{S}} \\
 x_{p1} &= \frac{1}{1 + \frac{\mu_m \mu_p S^2 - (Q_{p11} Q_{m11} + Q_{p12} Q_{m21})}{(Q_{p11} Q_{m12} + Q_{p12} Q_{m22})}} \quad \text{and} \quad x_{p2} = \frac{1}{1 + \frac{\mu_m \mu_p S^2 - (Q_{p21} Q_{m12} + Q_{p22} Q_{m22})}{(Q_{p21} Q_{m11} + Q_{p22} Q_{m21})}} \\
 x_{m1} &= \frac{1}{1 + \frac{\mu_m \mu_p S^2 - (Q_{m11} Q_{p11} + Q_{m12} Q_{p21})}{(Q_{m11} Q_{p12} + Q_{m12} Q_{p22})}} \quad \text{and} \quad x_{m2} = \frac{1}{1 + \frac{\mu_m \mu_p S^2 - (Q_{m21} Q_{p12} + Q_{m22} Q_{p22})}{(Q_{m21} Q_{p11} + Q_{m22} Q_{p21})}}.
 \end{aligned}$$

1085 E.2 Coexistence steady state with facultative hosts ($r_{p_i} \geq 0$)

The coexistence steady state $(p_1, \dots, p_M, m_1, \dots, m_N)$, that we write (\mathbf{p}, \mathbf{m}) with $\mathbf{p} = (p_1, \dots, p_M)$
 and $\mathbf{m} = (m_1, \dots, m_N)$, will satisfy the following problem:

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

1086 Combining the two systems, we obtain

$$1087 \quad \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_m \mu_p} \mathbf{m} = S^2 \mathbf{m} - S \frac{\mathbf{Q}_m}{\mu_m} \mathbf{p}_0 \quad \text{and} \quad \frac{\mathbf{Q}_p \mathbf{Q}_m}{\mu_p \mu_m} \mathbf{p} = S^2 (\mathbf{p} - \mathbf{p}_0).$$

We can reformulate the system as follows

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

where $\mathbf{A}_p = \frac{\mathbf{Q}_p \mathbf{Q}_m}{\mu_p \mu_m}$, $\mathbf{A}_m = \frac{\mathbf{Q}_m \mathbf{Q}_p}{\mu_m \mu_p}$ and $\mathbf{q}_0 = \frac{\mathbf{Q}_m}{\mu_m} \mathbf{p}_0$. Now assuming that S^2 is neither in the
 spectrum of \mathbf{A}_p nor \mathbf{A}_m , we get that

$$\mathbf{p} = S^2 (S^2 I - \mathbf{A}_p)^{-1} \mathbf{p}_0 \quad \text{and} \quad \mathbf{m} = S (S^2 I - \mathbf{A}_m)^{-1} \mathbf{q}_0.$$

Case of two hosts and two symbionts ($N = M = 2$) In this case we characterize S^2 with
 the positive root of a fourth order polynomial. Indeed,

$$\begin{aligned}
 \mathbf{p} &= S^2 (S^2 I - \mathbf{A}_p)^{-1} \mathbf{p}_0 = S^2 \frac{(S^2 I - (\mathbf{A}_p - \text{Tr}(\mathbf{A}_p) I))}{\det(S^2 I - \mathbf{A}_p)} \mathbf{p}_0 = S^2 \frac{S^2 \mathbf{p}_0 + (\mathbf{A}_p - \text{Tr}(\mathbf{A}_p) I) \mathbf{p}_0}{S^4 - \text{Tr}(\mathbf{A}_p) S^2 + \det(\mathbf{A}_p)}, \\
 \mathbf{m} &= S (S^2 I - \mathbf{A}_p)^{-1} \mathbf{q}_0 = S \frac{(S^2 \mathbf{q}_0 + (\mathbf{A}_m - \text{Tr}(\mathbf{A}_m) I) \mathbf{q}_0)}{S^4 - \text{Tr}(\mathbf{A}_p) S^2 + \det(\mathbf{A}_p)},
 \end{aligned}$$

because $\text{Tr}(\mathbf{Q}_p \mathbf{Q}_m) = \text{Tr}(\mathbf{Q}_m \mathbf{Q}_p)$ and $\det(\mathbf{Q}_p \mathbf{Q}_m) = \det(\mathbf{Q}_m \mathbf{Q}_p)$. Thus from the definition of
 S , we show that S solves the following equation

$$\begin{aligned}
 S &= \frac{1}{d} \mathbf{e} \mathbf{p} + \mathbf{e} \mathbf{m} \\
 &= \frac{S^2}{d} \mathbf{e} \left(\frac{S^2 \mathbf{p}_0 + (\mathbf{A}_p - \text{Tr}(\mathbf{A}_p) I) \mathbf{p}_0}{S^4 - \text{Tr}(\mathbf{A}_p) S^2 + \det(\mathbf{A}_p)} \right) + S \mathbf{e} \left(\frac{S^2 \mathbf{q}_0 + (\mathbf{A}_m - \text{Tr}(\mathbf{A}_m) I) \mathbf{q}_0}{S^4 - \text{Tr}(\mathbf{A}_p) S^2 + \det(\mathbf{A}_p)} \right).
 \end{aligned}$$

Thus, S is the positive root of the following fourth order polynomial

$$S^4 - \frac{1}{d} \mathbf{e} \mathbf{p}_0 S^3 - (\text{Tr}(\mathbf{A}_p) + \mathbf{e} \mathbf{q}_0) S^2 - \frac{1}{d} \mathbf{e} (\mathbf{A}_p - \text{Tr}(\mathbf{A}_p) I) \mathbf{p}_0 S + \det(\mathbf{A}_p) + \mathbf{e} (\mathbf{A}_m - \text{Tr}(\mathbf{A}_m) I) \mathbf{q}_0 = 0.$$

1088 Note that when $\mathbf{p}_0 = 0$, we recover the previous equation for S .

1089 **F Analysis of the one host and multiple competing sym-** 1090 **bionts case**

1091 We consider the case in which one host is associated with N symbionts m_1, \dots, m_N , which
1092 compete between each other. The corresponding differential equation system, is given by:

$$1093 \begin{cases} \frac{dp}{dt} = r_p + \frac{p}{\frac{p}{d} + \sum_{i=1}^N m_i} \left(q_{hp} \left(\sum_{i=1}^N \frac{\alpha_i}{d} m_i \right) - q_{cp} \left(\sum_{i=1}^N \beta_i m_i \right) \right) - \mu_p p^2, \\ \frac{dm_i}{dt} = \frac{p m_i}{\frac{p}{d} + \sum_{i=1}^N m_i} \left(q_{cm} \beta_i - q_{hm} \frac{\alpha_i}{d} - \sum_{j \neq i} c_{ji} m_j - \mu_m m_i \right). \end{cases} \quad (25)$$

The host, that might be obligate or facultative mutualists ($r_p \geq 0$), and symbionts exchange with the host at rates given by

$$Q_{p_i} = q_{hp} \frac{\alpha_i}{d} - q_{cp} \beta_i \quad \text{and} \quad Q_{m_i} = q_{cm} \beta_i - q_{hm} \frac{\alpha_i}{d}.$$

1094 **F.1 Steady state existence**

To compute the coexistence steady state (p, m_1, \dots, m_N) , that we write (p, \mathbf{m}) with $\mathbf{m} = (m_1, \dots, m_N)$, we first introduce the previous vectors, \mathbf{Q}_p , \mathbf{Q}_m , and \mathbf{p}_0

$$\mathbf{Q}_m = \begin{pmatrix} Q_{m_1} \\ \vdots \\ Q_{m_N} \end{pmatrix} \quad \text{and} \quad \mathbf{Q}_p = (Q_{p_1} \quad \cdots \quad Q_{p_N}) \quad \text{and} \quad p_0 = \frac{r_p}{\mu_p}.$$

We also introduce the following competition matrix \mathbf{C}_m

$$\mathbf{C}_m = \begin{pmatrix} \mu_m & c_{12} & \cdots & c_{1N} \\ c_{21} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & c_{(N-1)N} \\ c_{N1} & \cdots & c_{N(N-1)} & \mu_m \end{pmatrix},$$

1095 and let us denote $S = \frac{p}{d} + \sum_{i=1}^N m_i$.

From the system, we obtain that p, \mathbf{m} satisfies the following system of equation

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

1096 We will assume here that the competition strength between symbionts are all equal to c , that
1097 $c_{ij} = c$ for all $i \neq j$ in $\{1, \dots, N\}$. In this case the matrix $\mathbf{C}_m = (\mu_m - c)I + c\mathbf{1}$, where $\mathbf{1}$ is
1098 the matrix full of 1. We know that the eigenvalues of the $\mathbf{1}$ are 0 with multiplicity $N - 1$ and
1099 N with multiplicity 1. Thus the matrix \mathbf{C}_m is invertible if and only if

$$1100 \mu_m \neq c \quad \text{or} \quad \mu_m \neq (N + 1)c. \quad (26)$$

Moreover, we can compute its inverse as follow

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

1101 Under the previous assumption (26), by combining the two systems, we obtain

$$1102 \quad \frac{\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{Q}_p}{\mu_p} \mathbf{m} = S^2 \mathbf{m} - S \mathbf{C}_m^{-1} \mathbf{Q}_m p_0 \quad \text{and} \quad \frac{\mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m}{\mu_p} p = S^2 (p - p_0).$$

We can reformulate the system as follows:

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

1103 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

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

and we deduce that S is given by

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

1104 Finally, we get

$$1105 \quad p = p_0 + \frac{\frac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}}{\frac{S}{d} + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c(N-1)}} \quad \text{and} \quad \mathbf{m} = \frac{S}{\frac{S}{d} + \frac{\mathbf{e}\mathbf{Q}_m}{\mu_m + c(N-1)}} \mathbf{C}_m^{-1}\mathbf{Q}_m. \quad (27)$$

Special case of one obligate host ($r_p = 0$) **and two symbionts** ($N = 2$) In this case the previous formula become

$$S = \sqrt{\frac{\mathbf{Q}_p\mathbf{C}_m^{-1}\mathbf{Q}_m}{\mu_p}} = \sqrt{\frac{1}{\mu_p(\mu_m^2 - c^2)} \left((Q_{p1}Q_{m1} + Q_{p2}Q_{m2})\mu_m - c(Q_{p1}Q_{m2} + Q_{p2}Q_{m1}) \right)},$$

1106 and

$$1107 \quad p^* = \frac{S^2}{\frac{S}{d} + \frac{(Q_{m1} + Q_{m2})}{\mu_m + c}} \quad \text{and} \quad m_i^* = \frac{S}{\frac{S}{d} + \frac{(Q_{m1} + Q_{m2})}{\mu_m + c}} \frac{\mu_m Q_{mi} - cQ_{mj}}{(\mu_m^2 - c^2)}. \quad (28)$$

So the coexistence steady state exists if

$$c \leq \mu_m \min \left(1, \frac{Q_{m2}}{Q_{m1}}, \frac{Q_{m1}}{Q_{m2}}, \frac{Q_{p1}Q_{m1} + Q_{p2}Q_{m2}}{Q_{p1}Q_{m2} + Q_{p2}Q_{m1}} \right).$$

Special case with similar symbionts We assume here that symbionts are similar in the sense that the exchange rate are identical among symbionts, that is $Q_{pi} = Q_p$ and $Q_{mi} = Q_m$ for all $i \in \{1, \dots, N\}$. In this case the previous formula become

$$S_N = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d}\right)^2 + \frac{Q_m N}{\mu_m + c(N-1)}p_0 + \frac{Q_p Q_m N}{\mu_p(\mu_m + c(N-1))}},$$

and

$$p^* = p_0 + \frac{\frac{Q_p Q_m N}{\mu_p(\mu_m + c(N-1))}}{\frac{S_N}{d} + \frac{Q_m N}{\mu_m + c(N-1)}} \quad \text{and} \quad m_i^* = \frac{\frac{S_N Q_m}{\mu_m + c(N-1)}}{\frac{S_N}{d} + \frac{Q_m N}{\mu_m + c(N-1)}}.$$

1108 F.2 Stability of the steady state

Case of N similar symbionts We will show that the community of N similar symbionts is stable if and only if the competition between them is weak, such that

$$c < \mu_m.$$

1109 This inequality means that competition strength should be smaller than the maintenance
1110 cost. Actually, in this case, we can compute the Jacobian J_N around the steady state

1111 $(p^*, m_1^*, \dots, m_N^*)$:

$$1112 \quad J_N = \begin{pmatrix} j_p & b & \cdots & \cdots & b \\ a & j_m & e & \cdots & e \\ \vdots & e & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & e \\ a & e & \cdots & e & j_m \end{pmatrix} \quad \text{where} \quad \begin{cases} j_p = -\frac{p^* m^* N Q_p}{d S_N^2} - \mu_p p^* < 0 \\ b = \frac{(p^*)^2 Q_p}{d S_N^2} > 0 \\ a = \frac{N (m^*)^2 Q_m}{S_N^2} > 0 \\ j_m = -\frac{p^* m^* Q_m}{S_N^2} - \mu_m m^* < 0 \\ e = -\frac{p^* m^* Q_m}{S_N^2} - c m^* = j_m + (\mu_m - c) m^* < 0. \end{cases} \quad (29)$$

From the structure of the matrix, we can show that $j_m - e = (c - \mu_m) m^*$ is an eigenvalue of multiplicity $N - 1$ of the jacobian matrix J . Thus the characteristic polynomial of J can be factorize as follows

$$\det(J - \lambda I) = (\lambda - (c - \mu_m) m^*)^{N-1} (\lambda^2 + A\lambda + B),$$

where

$$A = -\text{Tr}(J) + (N - 1)(j_m - e) = -j_p - j_m - e(N - 1) > 0 \quad \text{and} \\ B = \frac{(-1)^{N+1} \det(J)}{(-(j_m - e))^{N-1}} = j_p(j_m + e(N - 1)) - 2bc > 0.$$

The coefficient A and B are positive, so the eigenvalues of the Jacobian are all negative if and only if the inequality

$$c < \mu_m$$

1113 holds true.

1114 **F.3 Stability of a community of native symbionts against an invasive** 1115 **symbiont**

1116 We here look at the stability of a host with $N \geq 1$ similar symbionts, in the presence of an
1117 invasive symbiont with exchange rates Q_{p_i} and Q_{m_i} . The competition strength c_{N_i} between
1118 the invader and the community might be different from the competition strength inside the
1119 community ($c = c_{nn}$), that is $c \neq c_{N_i}$. We here look at two particular cases: A community
1120 of only one symbiont (the parameter c does not occur here), and a community with $N > 1$
1121 similar symbionts. In this situations, the stability analysis needs to take into account the
1122 change in dynamics due to the presence of the invasive symbiont.

1123 **Stability of a single symbiont: the exclusion steady states $(p^*, m^*, 0)$** We her look
1124 at the case of in which a single symbiont is considered in association with a single host.
1125 In a context of multi symbiont competing with each other, it corresponds to the exclusion
1126 steady state. The definition of this state is given by (12) in section B. Linearizing around the
1127 $(p^*, m^*, 0)$ steady state, we obtain the Jacobian matrix J_{s1} :

$$1128 \quad J_{s1} = \left(\begin{array}{c|c} J(p^*, m^*) & B_1 \\ \hline 0 & a_i \end{array} \right) \quad \text{where } a_i = \frac{Q_{m_i} p^*}{S_1} - c_{N_i} m^*. \quad (30)$$

The Jacobian $J(p^*, m^*)$ is defined by (14) and B_1 is a vector which depends on p^* and m^* . From the analysis of section B, we know that the eigenvalues of $J(p^*, m^*)$ are negative, thus the exclusion steady state is stable if and only if

$$c_{N_i} > \frac{Q_{m_i}}{Q_m} \mu_m.$$

1129 **Competitive exclusion and coexistence** When considering a system of two competing
1130 symbionts (native symbiont m_n and an invasive symbiont m_i competing with strength $c =$
1131 $c_{m_{in}} = c_{m_{ni}}$) and a single host, then three possible steady states might exist: two exclusion
1132 steady states, $(p_n^*, m_n^*, 0)$ and $(p_i^*, 0, m_i^*)$, and a coexistence steady state (p_{ni}^*, m_n^*, m_i^*) . De-
1133 pending on the competition strength between the symbionts c and the exchange rates between
1134 the host and the symbionts, Q_{p_i} , Q_{p_n} , Q_{m_i} and Q_{m_n} , which are defined by α and β , we have
1135 two regimes: the competitive exclusion regime (i.e., stability of at least one exclusion steady
1136 state) and the coexistence regime (i.e., stability of the coexistence steady state).

Competitive exclusion occurs when the competition strength is large, that is

$$c > \mu_m \min \left(\frac{Q_{m_i}}{Q_{m_n}}, \frac{Q_{m_n}}{Q_{m_i}} \right).$$

Conversely, coexistence occurs when the competition is weak, that is when the host is obligate
 $r_p = 0$

$$c < \mu_m \min \left(1, \frac{Q_{m_i}}{Q_{m_n}}, \frac{Q_{m_n}}{Q_{m_i}}, \frac{Q_{p_n} Q_{m_n} + Q_{p_i} Q_{m_i}}{Q_{p_n} Q_{m_i} + Q_{p_i} Q_{m_n}} \right).$$

1137 **Harmful and beneficial symbiont with competition** We have seen that depending on the
1138 strength of competition coexistence or competitive exclusion can occur. In order to understand
1139 whether an invasive symbiont is harmful or beneficial to the native host, we compare the
1140 biomass of host at equilibrium in the absence of the invasive symbiont p_n^* , that is, when the
1141 host is associated only with its native symbiont, and the biomass of the host with the invasive
1142 symbiont in the two alternative cases: exclusion steady state p_i^* in which only the invasive
1143 symbiont persist or coexistence steady state p_{ni}^* .

1144 From the formulae (27) and (28), we can see that if competition is weak enough the
1145 coexistence state exists. In this case, we can compare the biomass of the host with its native
1146 symbiont and its biomass in presence of both a native and an invasive symbionts. Depending
1147 on the mutualistic quality of the invasive symbiont, quantified through α_{in} , we can see from
1148 Fig. C.2 that the biomass of the host with the two symbiont is larger than its biomass only
1149 with its native symbiont if the invasive symbiont is a good mutualist ($\alpha_{in} > \alpha_{in}^*$ defined
1150 by Eq. (6)). In this case the symbiont is called beneficial to the host. Conversely, if the
1151 mutualistic quality of the symbiont is low, the biomass of the host in the presence of the
1152 symbiont is reduced below the biomass of the host observed when the host is associated only
1153 with its native symbiont, and the introduced symbiont is called harmful.

1154 If competition is strong ($c \geq \mu_m$), in order to be beneficial to the host, the introduced
1155 symbiont should have a higher mutualistic quality than when competition is low.

1156 **Special case of obligate host** ($r_p = 0$). In this case, we can compute the steady state and
 1157 we obtain

$$\begin{aligned}
 p_{ni}^*(\alpha_{nn}, \alpha_{in}) &= \frac{\sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}} \sqrt{\frac{\mu_m^2}{\mu_m^2 - c^2}} \sqrt{1 + \frac{q_p q_m}{Q_p Q_m} - \frac{c}{\mu_m} \left(\frac{q_m}{Q_m} + \frac{q_p}{Q_p} \right)}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}} \frac{\sqrt{\frac{\mu_m - c}{\mu_m + c}} \left(1 + \frac{q_m}{Q_m} \right)}{\sqrt{1 + \frac{q_p q_m}{Q_p Q_m} - \frac{c}{\mu_m} \left(\frac{q_m}{Q_m} + \frac{q_p}{Q_p} \right)}}} \\
 &= p_n^*(\alpha_{nn}) \frac{\left(\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}} \right) \sqrt{\frac{\mu_m^2}{\mu_m^2 - c^2}} \sqrt{1 + \frac{q_p q_m}{Q_p Q_m} - \frac{c}{\mu_m} \left(\frac{q_m}{Q_m} + \frac{q_p}{Q_p} \right)}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}} \frac{\sqrt{\frac{\mu_m - c}{\mu_m + c}} \left(1 + \frac{q_m}{Q_m} \right)}{\sqrt{1 + \frac{q_p q_m}{Q_p Q_m} - \frac{c}{\mu_m} \left(\frac{q_m}{Q_m} + \frac{q_p}{Q_p} \right)}}},
 \end{aligned}$$

1159 where $p_n^*(\alpha_{nn})$ is the biomass of the native host at equilibrium only with its native symbiont:

$$p_n^*(\alpha_{nn}) = \frac{\sqrt{\frac{Q_p Q_m}{\mu_m \mu_p}}}{\frac{1}{d} + \sqrt{\frac{Q_m \mu_p}{\mu_m Q_p}}}.$$

1161 **Stability of a community of $N > 1$ symbionts** The Jacobian J_{sN} of the system around
 1162 the steady state $(p^*, m_1^*, \dots, m_N^*, 0)$ becomes

$$J_{sN} = \left(\begin{array}{c|c} J_N & B \\ \hline 0 & a_i \end{array} \right) \quad \text{where } a_i = \frac{Q_{mi} p^*}{S_N} - c_{Ni} \sum_{k=1}^N m_k^* = \frac{Q_{mi} p^*}{S_N} - c_{Ni} (S_N - \frac{p^*}{d}). \quad (31)$$

From the previous computation, we know that the eigenvalues of J_N are negative if and only if $c \leq \mu_m$. Thus the community of N symbionts is stable against an invader if and only if

$$c_{Ni} \geq \frac{Q_{mi}}{Q_m} \left(\frac{N-1}{N} c + \frac{\mu_m}{N} \right).$$

1164 If the invader is a better mutualist, that is $Q_{mi} \leq Q_m$, then the community is not really
 1165 threaten if the competition strength between the invader is similar as the competition strength
 1166 inside the community, that is $c \approx c_{Ni}$. Conversely, if the invader is more parasitic than the
 1167 community, that is $Q_{mi} > Q_m$, the competition pressure of the community should increase
 1168 on the invader compared to the competition inside the community.

1169 **G Analysis of the one symbiont and multiple competing** 1170 **hosts case**

1171 A similar analysis to what shown in section F can be carried out to find conditions for the
 1172 coexistence of multiple competing hosts sharing a common symbiont.

When adding competition between hosts, that is described by the following matrix \mathbf{C}_p

$$\mathbf{C}_p = \begin{pmatrix} \mu_p & c_p & \cdots & c_p \\ c_p & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & c_p \\ c_p & \cdots & c_p & \mu_p \end{pmatrix},$$

the steady state (p_1, \dots, p_N, m) will satisfy the following problem:

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

where now \mathbf{p}_0 depends on the competition between hosts and it is defined by

$$\mathbf{p}_0 = \mathbf{C}_p^{-1} \begin{pmatrix} r_{p_1} \\ \vdots \\ r_{p_N} \end{pmatrix}.$$

Let us remark that \mathbf{p}_0 is the coexistence steady state of N facultative hosts in competition. It is an actual steady state of our problem only if its components are all positive, that requires the following assumption

$$c_p \leq \frac{\mu_p}{N-1}.$$

1173 We immediately recover that if competition between hosts is too strong, coexistence is not
1174 possible.

1175 Combining the two systems, we obtain:

$$1176 \quad \frac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m} m = S^2 m - S \frac{\mathbf{Q}_m}{\mu_m} \mathbf{p}_0 \quad \text{and} \quad \frac{\mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{Q}_m}{\mu_m} \mathbf{p} = S^2 (\mathbf{p} - \mathbf{p}_0).$$

We can reformulate the system as follows:

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

1177 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 $\mathbf{A}^k = \left(\frac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m} \right)^k \mathbf{A}$ for any $k \geq 2$, we

deduce that

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

We can compute \mathbf{p} as follows

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

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

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

Special case of two obligate hosts ($r_p = 0$) and one symbiont ($N = 2$) In this case the previous formula become

$$S = \sqrt{\frac{\mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p}{\mu_m}} = \sqrt{\frac{1}{\mu_m (\mu_p^2 - c_p^2)} \left((Q_{p_1} Q_{m_1} + Q_{p_2} Q_{m_2}) \mu_p - c_p (Q_{p_1} Q_{m_2} + Q_{p_2} Q_{m_1}) \right)},$$

and

$$p_i^* = \frac{S}{S + \frac{(Q_{p_1} + Q_{p_2})}{(\mu_p + c_p)d}} \frac{\mu_p Q_{p_i} - c_p Q_{p_j}}{(\mu_p^2 - c_p^2)} \quad \text{and} \quad m^* = \frac{S^2}{S + \frac{(Q_{p_1} + Q_{p_2})}{(\mu_p + c_p)d}}.$$

So the coexistence steady state exists if and only if

$$Q_{p_1} > 0 \quad \text{and} \quad Q_{p_2} > 0,$$

and

$$c_p \leq \mu_p \min \left(1, \frac{Q_{p_2}}{Q_{p_1}}, \frac{Q_{p_1}}{Q_{p_2}}, \frac{Q_{p_1} Q_{m_1} + Q_{p_2} Q_{m_2}}{Q_{p_1} Q_{m_2} + Q_{p_2} Q_{m_1}} \right).$$

1178 **Stability of the steady state**

With the description of the steady state we can compute the Jacobian of the system around the steady state (p_1, \dots, p_N, m) as follows

$$J_{p_N} = \left(\begin{array}{cccc|c} j_{p_1} & e_1 & \cdots & e_1 & b_1 \\ e_2 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \ddots & \ddots & e_{N-1} & \vdots \\ e_N & \cdots & e_N & j_{p_N} & b_N \\ \hline c_1 & \cdots & \cdots & c_N & j_m \end{array} \right) \quad \text{where} \quad \begin{aligned} j_m &= -\frac{\mathbf{Q}_p \mathbf{p}}{S^2} m - \mu_m m < 0 \\ b_i &= \frac{p_i Q_{p_i} \mathbf{e} \mathbf{p}}{S^2 d} > 0 \\ c_i &= \frac{Q_{m_i} m}{S^2} \left(S - \frac{1}{d} p_i \right) > 0 \\ j_{p_i} &= -\frac{Q_{p_i} p_i m}{d S^2} - \mu_p p_i < 0 \\ e_i &= -\frac{Q_{p_i} p_i m}{d S^2} - c p_i < 0. \end{aligned}$$

1179 If the hosts are identical and the symbiont provides nutrients at the same rate for every host,
1180 then we can prove as in section F.2, that the steady state is stable if and only if $c < \mu_p$.

H Analysis of the multiple competing symbionts and multiple competing hosts case

We here consider M competing hosts and N competing symbionts that may exchange resources; We obtain the following system

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

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

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

Let us define the two exchange matrices \mathbf{Q}_p and \mathbf{Q}_m

$$\mathbf{Q}_p = \begin{pmatrix} Q_{p_{11}} & \cdots & Q_{p_{1N}} \\ \vdots & & \vdots \\ Q_{p_{M1}} & \cdots & Q_{p_{MN}} \end{pmatrix} \quad \text{and} \quad \mathbf{Q}_m = \begin{pmatrix} Q_{m_{11}} & \cdots & Q_{m_{1M}} \\ \vdots & & \vdots \\ Q_{m_{N1}} & \cdots & Q_{m_{NM}} \end{pmatrix},$$

and the two competition matrices \mathbf{C}_m and \mathbf{C}_p

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

Let us denote $S = \frac{1}{d} \sum_{i=1}^M p_i + \sum_{j=1}^N m_j$, $\mathbf{p} = (p_1, \dots, p_M)$ and $\mathbf{m} = (m_1, \dots, m_N)$. Since the competition terms are identical among hosts and symbionts, we can reformulate the matrices \mathbf{C}_p and \mathbf{C}_m using the identity matrix I and the matrix with all ones $\mathbf{1}$:

$$\mathbf{C}_p = (\mu_p - c_p) \left(I + \frac{c_p}{\mu_p - c_p} \mathbf{1} \right) \quad \text{and} \quad \mathbf{C}_m = (\mu_m - c_m) \left(I + \frac{c_m}{\mu_m - c_m} \mathbf{1} \right).$$

As soon as $\mu_p \neq c_p$ and $\mu_m \neq c_m$, the competition matrices are invertible, with inverse satisfying

$$\mathbf{C}_p^{-1} = \frac{1}{\mu_p - c_p} \left(I - \frac{c_p}{\mu_p + c_p(M-1)} \mathbf{1} \right) \quad \text{and} \quad \mathbf{C}_m^{-1} = \frac{1}{\mu_m - c_m} \left(I - \frac{c_m}{\mu_m + c_m(N-1)} \mathbf{1} \right).$$

Then, let us denote

$$\mathbf{p}_0 = \mathbf{C}_p^{-1} \begin{pmatrix} r_{p_1} \\ \vdots \\ r_{p_M} \end{pmatrix}.$$

The quantity \mathbf{p}_0 , which is the coexistence steady state of facultative hosts alone (in absence of symbionts), is non negative if the competition strength is not too large, that is

$$c_p < \mu_p \min \left\{ \frac{1}{1 + \frac{r_p - r_{p_i}}{r_{p_i}} M}, \text{ s.t. } \frac{M}{r_p} > r_{p_i} > 0, i \in \{1, \dots, M\} \right\},$$

1186 where $\bar{r}_p = \frac{1}{M} \sum_{j=1}^M r_{p_j}$.

1187 In particular, if the host have the same growth rate $r_p \geq 0$, the quantity \mathbf{p}_0 satisfies

$$1188 \quad \mathbf{p}_0 = p_0 \frac{\mu_p}{\mu_p + c_p(M-1)} \begin{pmatrix} 1 \\ \vdots \\ 1 \end{pmatrix}, \quad \text{where } p_0 = \frac{r_p}{\mu_p}.$$

1189 Using these new notations, we can write the previous system as follows:

$$1190 \quad \begin{cases} \frac{d\mathbf{p}}{dt} = \mathbf{p} \cdot \left(\frac{\mathbf{Q}_p \mathbf{m}}{S} - \mathbf{C}_p(\mathbf{p} - \mathbf{p}_0) \right), \\ \frac{d\mathbf{m}}{dt} = \mathbf{m} \cdot \left(\frac{\mathbf{Q}_m \mathbf{p}}{S} - \mathbf{C}_m \mathbf{m} \right), \end{cases} \quad (32)$$

1191 where \cdot represent the Hadamard product.

1192 H.1 Coexistence steady state

The coexistence steady state of the system of Eq. (32) is given by

$$\begin{cases} \frac{\mathbf{Q}_p \mathbf{m}}{S} = \mathbf{C}_p(\mathbf{p} - \mathbf{p}_0), \\ \frac{\mathbf{Q}_m \mathbf{p}}{S} = \mathbf{C}_m \mathbf{m}. \end{cases}$$

1193 H.1.1 Coexistence with obligate hosts ($r_p = 0$)

1194 Combining the two systems we show that, if it exists, S^2 is the positive eigenvalue of the
 1195 matrix $\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p$ and \mathbf{m} is its positive eigenvector. Even if \mathbf{Q}_m and \mathbf{Q}_p are positive
 1196 matrices, due to the competition matrices \mathbf{C}_p and \mathbf{C}_m , the product might not be positive.
 1197 When it exists, the eigenpair satisfying the following system corresponds to

$$1198 \quad \mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{m} = S^2 \mathbf{m} \quad \text{and} \quad \mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{p} = S^2 \mathbf{p}.$$

1199 **Special case with $M = 2$ obligate hosts and $N = 2$ symbionts.** In this case the matrices
 1200 are of size 2×2 and we can compute the second order characteristic polynomial:

$$1201 \quad S^2 - \text{Tr}(\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p) S + \det(\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p).$$

1202 Its positive root corresponds to S^2 , that is

$$1203 \quad S^2 = \frac{\text{Tr}(\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p)}{2} + \frac{1}{2} \sqrt{(\text{Tr}(\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p))^2 - 4 \det(\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p)}.$$

1204 From the expression of the competition matrices, we can compute the trace and determinant
 1205 as follows

$$1206 \quad \begin{aligned} \text{Tr}(\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p) &= \text{Tr} \left(\frac{1}{\mu_m - c_m} \left(I - \frac{c_m}{\mu_m + c_m} \mathbf{1} \right) \mathbf{Q}_m \frac{1}{\mu_p - c_p} \left(I - \frac{c_p}{\mu_p + c_p} \mathbf{1} \right) \mathbf{Q}_p \right) \\ &= \frac{1}{(\mu_m - c_m)(\mu_p - c_p)} \text{Tr} \left(\left(\mathbf{Q}_m - \frac{c_m}{\mu_m + c_m} \mathbf{1} \mathbf{Q}_m \right) \left(\mathbf{Q}_p - \frac{c_p}{\mu_p + c_p} \mathbf{1} \mathbf{Q}_p \right) \right) \\ &= \frac{1}{(\mu_m - c_m)(\mu_p - c_p)} \left(\text{Tr}(\mathbf{Q}_m \mathbf{Q}_p) - \frac{c_m}{\mu_m + c_m} \text{Tr}(\mathbf{1} \mathbf{Q}_m \mathbf{Q}_p) \right. \\ &\quad \left. - \frac{c_p}{\mu_p + c_p} \text{Tr}(\mathbf{Q}_m \mathbf{1} \mathbf{Q}_p) + \frac{c_m}{\mu_m + c_m} \frac{c_p}{\mu_p + c_p} \text{Tr}(\mathbf{1} \mathbf{Q}_m \mathbf{1} \mathbf{Q}_p) \right) \\ \det(\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p) &= \frac{\det(\mathbf{Q}_m \mathbf{Q}_p)}{(\mu_m^2 - c_m^2)(\mu_p^2 - c_p^2)}. \end{aligned} \quad (33)$$

1207 The condition on the discriminant provides a condition on the competition terms c_m and c_p .
 1208 In particular, if $c_p = 0$, then we have an explicit condition on c_m , that is the discriminant is
 1209 positive if and only if $c_m \leq c_m^*$ where c_m^* depends on the matrices \mathbf{Q}_m and \mathbf{Q}_p as it satisfies

$$1210 \frac{\mu_m + c_m}{\mu_m - c_m} \left(\frac{1}{2} \left(\text{Tr}(\mathbf{Q}_m \mathbf{Q}_p) - \frac{c_m}{\mu_m + c_m} \text{Tr}(\mathbf{1} \mathbf{Q}_m \mathbf{Q}_p) \right) \right)^2 = \det(\mathbf{Q}_m \mathbf{Q}_p).$$

1211 In particular, we see that $c_m^* < \mu_m$.

1212 In addition, the matrices $\mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m$ and $\mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p$ might be non positive and
 1213 the existence of positive eigenpair truly depend on the competition parameters.

1214 Thus, if the competition parameters are large enough, that is $c_p \geq \mu_p$ or $c_m \geq \mu_m$, then
 1215 the coexistence steady state does not exist or is unstable.

1216 H.1.2 Coexistence with facultative hosts ($r_p > 0$)

In this case, the system can be reformulated as follows

$$(S^2 I - \mathbf{A}) \mathbf{p} = S^2 \mathbf{p}_0 \quad \text{and} \quad (S^2 I - \tilde{\mathbf{A}}) \mathbf{m} = S \mathbf{q}_0,$$

where $\mathbf{A} = \mathbf{C}_p^{-1} \mathbf{Q}_p \mathbf{C}_m^{-1} \mathbf{Q}_m$, $\tilde{\mathbf{A}} = \mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{C}_p^{-1} \mathbf{Q}_p$ and $\mathbf{q}_0 = \mathbf{C}_m^{-1} \mathbf{Q}_m \mathbf{p}_0$. As long as S^2 is not
 an eigenvalue of \mathbf{A} and $\tilde{\mathbf{A}}$, we can solve the previous linear system. Then using the definition
 of $S = \mathbf{e} \mathbf{p} / d + \mathbf{e} \mathbf{m}$, S should satisfies the following equation

$$S = \frac{S^2}{d} \mathbf{e} (S^2 I - \mathbf{A})^{-1} \mathbf{p}_0 + S (S^2 I - \tilde{\mathbf{A}})^{-1} \mathbf{q}_0.$$

Special case with $M = 2$ facultative hosts and $N = 2$ symbionts. Since \mathbf{A} and $\tilde{\mathbf{A}}$ have
 same trace and determinant and they are of dimension 2, we can show that

$$(S^2 I - \mathbf{A})^{-1} = \frac{S^2 I + (\mathbf{A} - \text{Tr}(\mathbf{A}) I)}{S^4 - \text{Tr}(\mathbf{A}) S^2 + \det(\mathbf{A})} \quad \text{and} \quad (S^2 I - \tilde{\mathbf{A}})^{-1} = \frac{S^2 I + (\tilde{\mathbf{A}} - \text{Tr}(\mathbf{A}) I)}{S^4 - \text{Tr}(\mathbf{A}) S^2 + \det(\mathbf{A})}.$$

We deduce that

$$\mathbf{p} = S^2 \frac{S^2 \mathbf{p}_0 + (\mathbf{A} - \text{Tr}(\mathbf{A}) I) \mathbf{p}_0}{S^4 - \text{Tr}(\mathbf{A}) S^2 + \det(\mathbf{A})} \quad \text{and} \quad \mathbf{m} = S \frac{S^2 \mathbf{q}_0 + (\tilde{\mathbf{A}} - \text{Tr}(\mathbf{A}) I) \mathbf{q}_0}{S^4 - \text{Tr}(\mathbf{A}) S^2 + \det(\mathbf{A})}.$$

Thus, from the definition of S , we show that S is the positive root of the following fourth
 order polynomial

$$S^4 - \frac{1}{d} \mathbf{e} \mathbf{p}_0 S^3 - (\text{Tr}(\mathbf{A}) + \mathbf{e} \mathbf{q}_0) S^2 - \frac{1}{d} \mathbf{e} (\mathbf{A} - \text{Tr}(\mathbf{A}) I) \mathbf{p}_0 S - \mathbf{e} (\tilde{\mathbf{A}} - \text{Tr}(\mathbf{A}) I) \mathbf{q}_0 = 0.$$

1217 H.2 Stability analysis

The Jacobian of the system around the coexistence steady state $(p_1, \dots, p_M, m_1, \dots, m_N)$ can
 be computed as follows

$$J = \begin{pmatrix} J_p & B \\ C & J_m \end{pmatrix} \quad \text{where} \quad \begin{aligned} J_m &= -\mathbf{m} \cdot \left(\frac{\mathbf{Q}_m \mathbf{p}}{S^2} + \mathbf{C}_m \right) < 0 \\ B &= \frac{\mathbf{p}}{S^2} \cdot (S \mathbf{Q}_p - \mathbf{Q}_p \mathbf{m}) \\ C &= \frac{\mathbf{m}}{S^2} \cdot \left(S \mathbf{Q}_m - \frac{1}{d} \mathbf{Q}_m \mathbf{p} \right) \\ J_p &= -\mathbf{p} \cdot \left(\frac{\mathbf{Q}_p \mathbf{m}}{S^2} + \mathbf{C}_p \right) < 0. \end{aligned}$$

1218 In this situation, the stability analysis is more complex as the stability of the coexistence
 1219 steady state will truly depend on all the interactions terms of the system (i.e., on the nutrient
 1220 exchange rates as well as on competition).

I Analysis of the model steady states and 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., $Q_{p_{kk}} = Q_p$ and $Q_{m_{kk}} = Q_m$ for $k \in \{1, 2\}$. Furthermore,

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

In contrast, the exchange between native and invasive species, i.e., $Q_{p_{kl}}$ and $Q_{m_{kl}}$ for $k \neq l$, may vary depending on the scenario: (−) the symbiont is harmful to the host, (0) no interaction between host and symbiont and (+) the symbiont is beneficial (see Table 1 and section C.3 for details on the scenarios). More specifically, for $k \neq l$ in $\{1, 2\}$ we have

$$Q_{p_{kl}} = \begin{cases} Q_p & \text{beneficial (+)} \\ 0 & \text{neutral (0)} \\ -q_p = -q_{cp} \beta < 0 & \text{harmful (-)} \end{cases} \quad \text{and} \quad Q_{m_{lk}} = \begin{cases} Q_m & \text{beneficial (+)} \\ 0 & \text{neutral (0)} \\ q_m = q_{cm} \beta > Q_m > 0 & \text{harmful (-)} \end{cases} \quad (34)$$

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

$$\begin{cases} \frac{dp_1}{dt} &= r_{p_1} p_1 + \frac{p_1}{\frac{p_1}{d} + \frac{p_2}{d} + m_1 + m_2} (m_1 Q_p + m_2 Q_{p_{12}}) - \mu_p p_1^2 - c_p p_2 p_1, \\ \frac{dm_1}{dt} &= \frac{p_1}{\frac{p_1}{d} + \frac{p_2}{d} + m_1 + m_2} (p_1 Q_m + p_2 Q_{m_{12}}) - \mu_m m_1^2 - c_m m_2 m_1, \\ \frac{dp_2}{dt} &= r_{p_2} p_2 + \frac{p_2}{\frac{p_1}{d} + \frac{p_2}{d} + m_1 + m_2} (m_2 Q_p + m_1 Q_{p_{21}}) - c_p p_1 p_2 - \mu_p p_2^2, \\ \frac{dm_2}{dt} &= \frac{p_2}{\frac{p_1}{d} + \frac{p_2}{d} + m_1 + m_2} (p_2 Q_m + p_1 Q_{m_{21}}) - c_m m_1 m_2 - \mu_m m_2^2. \end{cases} \quad (35)$$

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

$$\mathbf{Q}_p = \begin{pmatrix} Q_p & Q_{p_{12}} \\ Q_{p_{21}} & Q_p \end{pmatrix} \quad \text{and} \quad \mathbf{Q}_m = \begin{pmatrix} Q_m & Q_{m_{12}} \\ Q_{m_{21}} & Q_m \end{pmatrix},$$

the two interaction matrices \mathbf{C}_p and \mathbf{C}_m :

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

and the quantity $S = \frac{p_1}{d} + \frac{p_2}{d} + m_1 + m_2$.

Then, using the notation $\mathbf{p} = (p_1, p_2)$, $\mathbf{m} = (m_1, m_2)$, and $\mathbf{r}_p = (r_{p_1}, r_{p_2})$, the system (35) can be reformulated as

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

1231 I.1 Steady states of the system

1232 I.1.1 Exclusion steady states consisting of one host and one symbiont

1233 In our system, the steady state that comprises only one host and one symbiont always ex-
 1234 ists. Therefore there are four possible exclusion steady states: $(p_n^*, m_n^*, 0, 0)$, $(0, 0, p_i^*, m_i^*)$,
 1235 $(p_n^*, 0, 0, m_i^*)$ and $(0, m_n^*, p_i^*, 0)$. Due to our choice of parameters (i.e., with α_{nn} , α_{ii} , β_{nn} and
 1236 β_{ii} large enough), the steady state with only native species or only invasive species always
 1237 exist. However, the mixed steady states composed of either a native host with an invasive
 1238 symbiont, or an invasive host with a native symbiont, only exist when the cross-species re-
 1239 source exchange is beneficial (+) to the new host, while they do not exist if cross species
 1240 resource exchange is neutral (0) or harmful (-) to the new host.

1241 We note here that a harmful symbiont, with low mutualistic quality (α small) and that
 1242 corresponds to negative Q_p , can only survive on a host with high intrinsic growth rate, that
 1243 is a facultative mutualist with $Q_{p_{ij}} > -r_{p_j}$. If the host is an obligate mutualist, the mixed
 1244 steady state cannot exist with a harmful symbiont, because survival requires that $Q_{p_{ij}} > 0$.

When a mixed steady state exists, its stability depends on the interactions of the host
 with its original symbiont. To define this dependence more precisely, we compute the Jacobian
 matrix of the the steady state. For simplicity, we only look at (p_1, m_1) but the argument can
 be made valid for the other case by permuting the indices and considering indexes 1 and 2 to
 correspond to n and i . In the case we consider the Jacobian matrix given by

$$J = \left(\begin{array}{c|c} J(p_1^*, m_1^*) & B \\ \hline 0 & C \end{array} \right) \quad \text{where } C = \begin{pmatrix} Q_{p_{21}} \frac{m_1^*}{S} + r_p - c_p p_1^* & 0 \\ 0 & Q_{m_{21}} \frac{p_1^*}{S} - c_m m_1^* \end{pmatrix},$$

where $J(p_1^*, m_1^*)$ is defined by (14) in section B.2. From the analysis of Section B.2, we know
 that the matrix $J(p_1^*, m_1^*)$ has two negative eigenvalues. Moreover, from the expressions for
 the steady states p_1^* and m_1^* , we can show that

$$C = \begin{pmatrix} \left(\frac{Q_{p_{21}}}{Q_p} - \frac{c_p}{\mu_p} \right) p_1^* + \left(1 - \frac{Q_{p_{21}}}{Q_p} \right) p_0 & 0 \\ 0 & \left(\frac{Q_{m_{21}}}{Q_m} - c_m \right) m_1^* \\ \frac{p_0}{S^2 - \frac{Q_p Q_m}{\mu_p \mu_m}} \left(\left(1 - \frac{c_p}{\mu_p} \right) S^2 - \frac{Q_p Q_m}{\mu_p \mu_m} \left(1 - \frac{Q_{p_{21}}}{Q_p} \right) \right) & 0 \\ 0 & \left(\frac{Q_{m_{21}}}{Q_m} \mu_m - c_m \right) m_1^* \end{pmatrix}.$$

1245 We now consider the two separate cases of strong and weak competition between hosts.

Strong competition between hosts ($c_p \geq \mu_p$) **and symbionts** ($c_m \geq \mu_m$) When compe-
 1246 tion is strong, the non-mixed steady states $(p_n^*, m_n^*, 0, 0)$ and $(0, 0, p_i^*, m_i^*)$ are always stable.
 A mixed pair steady state with a beneficial symbiont (+) (i.e., steady states $(p_n^*, 0, 0, m_i^*)$ and
 1247 $(0, m_n^*, p_i^*, 0)$, when m_n/m_i is beneficial to p_i/p_n) are also always stable. A mixed pair steady
 state with a harmful symbiont (-) (i.e., when m_n/m_i is harmful to p_i/p_n), when it exists, is
 stable only if competition between hosts is very strong, that is

$$c_p \geq \mu_p + \frac{q_m}{\mu_m} \frac{(Q_p + q_p)}{S^2} > \mu_p, \quad \text{with } S = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d} \right)^2 + p_0 \frac{q_m}{\mu_m} - \frac{q_m q_p}{\mu_m \mu_p}}.$$

1246 Under strong competition, the system will converge towards one of these four steady states
 1247 in almost every scenario (see Fig. 3).

Weak competition between hosts. This case corresponds to $c_p \leq \mu_p$. Here, the steady states $(p_n^*, m_n^*, 0, 0)$ and $(0, 0, p_i^*, m_i^*)$, $(p_n^*, 0, 0, m_i^*)$ and $(0, m_n^*, p_i^*, 0)$ are stable if and only if

$$Q_{p21} < 0 \quad (36)$$

$$\frac{Q_{m21}}{Q_m} \mu_m - c_m \leq 0. \quad (37)$$

In other words, if competition between hosts is weak, and the native/invasive symbiont is very harmful to the invasive/native host (scenarios $(-, -)$, $(0, -)$ or $(+, -)$), then the steady states consisting of only native hosts and symbionts or of only invasive hosts and symbionts are stable.

The inequality (37) is always satisfied if the invasive/native symbiont does not benefit from the native/invasive host, i.e., $Q_{m21} = 0$, which corresponds to the scenario $(-, 0)$. This inequality can also be satisfied if the competition between symbionts is strong, i.e., $c_m > \mu_m$. So under strong competition between symbionts, the exclusion steady state is also stable in the scenarios $(-, +)$ and $(-, -)$. Otherwise, symbionts may coexist, as shown in the next section.

1.1.2 Inclusion steady states consisting of one host and two symbionts

The inclusion steady state that we consider in this section corresponds to the case where one host integrates the symbiont from the other host and excludes the other host. In our system, we have two possible steady states of this form $(p_n, 0, m_n, m_i)$ and $(0, p_i, m_n, m_i)$. They exist if and only if

$$Q_{p_{ij}} \geq -\frac{Q_p Q_m}{Q_{m_{ji}}} \text{ for } i \in \{1, 2\} \text{ and } j \neq i$$

and

$$c_m < \mu_m \min \left(1, \frac{Q_m}{Q_{m_{ji}}}, \frac{Q_{m_{ji}}}{Q_m}, \frac{Q_p Q_m + Q_{p_{ij}} Q_{m_{ji}}}{Q_p Q_{m_{ji}} + Q_{p_{ij}} Q_m} \right) \text{ for } i \in \{1, 2\} \text{ and } j \neq i.$$

Thus, the inclusion steady state with one host and two symbionts exists **competition between the symbionts is weak** and the invasive/native symbiont is not too harmful to the native/invasive host.

In this case, we can compute the Jacobian matrix to explore the stability of this steady state. Let us look at the inclusion of the invasive symbiont m_i by the native host p_n and its symbiont m_n , i.e., the steady state $(p_1^*, 0, m_1^*, m_2^*)$. The Jacobian is given by the matrix

$$J(p_1, 0, m_1, m_2) = \left(\begin{array}{c|c} J(p_1^*, m_1^*, m_2^*) & B \\ \hline 0 & C \end{array} \right) \text{ where } C = Q_{p21} \frac{m_1^*}{S} + Q_p \frac{m_2^*}{S} + r_p - c_p p_1^*.$$

The eigenvalues of the matrix $J(p_1^*, m_1^*, m_2^*)$ are negative if the competition between the symbionts is not too strong. In this case, the steady state is stable if and only if $C < 0$, which is equivalent to

$$\left((Q_{p21} \ Q_p) - \frac{c_p}{\mu_p} (Q_p \ Q_{p12}) \right) \frac{\mathbf{C}_m^{-1} \begin{pmatrix} Q_m \\ Q_{m21} \end{pmatrix}}{\frac{S}{d} + \frac{Q_m + Q_{m21}}{\mu_m + c_m}} + r_p \left(1 - \frac{c_p}{\mu_p} \right) < 0.$$

We now consider the two separate cases of strong and weak competition between hosts.

1267 **Strong competition between hosts.** If competition between hosts is strong, i.e., $c_p \geq \mu_p$,
 1268 the steady states $(p_n, 0, m_n, m_i)$ and $(0, p_i, m_n, m_i)$ are stable when it exists.

1269 **Weak competition between hosts.** If, on the other hand, the competition between hosts
 1270 is weak, i.e., $c_p \leq \mu_p \frac{Q_{p_{12}}}{Q_p}$, for stability we obtain the following inequality

$$1271 \quad Q_{p_{21}} < \frac{c_p}{\mu_p} Q_p - \left(r_p \frac{\frac{S}{d} + \frac{Q_m + Q_{m_{21}}}{\mu_m + c}}{\mu_m Q_m - c_m Q_{m_{21}}} \left(1 - \frac{c_p}{\mu_p} \right) + \left(Q_p - \frac{c_p}{\mu_p} Q_{p_{12}} \right) \frac{\mu_m Q_{m_{21}} - c_m Q_m}{\mu_m Q_m - c_m Q_{m_{21}}} \right).$$

1272 Thus, the inclusion steady state is stable only when the initial symbiont paired with the host is
 1273 very harmful to the other host, i.e., $Q_{p_{21}} < 0$, which corresponds to scenario $(-)$. Conversely,
 1274 this steady state is unstable as soon as $Q_{p_{21}} \geq 0$, i.e., the symbiont is either neutral (scenario
 1275 (0)) or beneficial (scenario $(+)$) to the other host. This scenario is presented in the next
 1276 section.

1277 I.1.3 Inclusion steady states consisting of two hosts and one symbiont

This inclusion steady state corresponds to the case where one symbiont supports the two
 hosts and excludes the other symbiont. In our system, we have two possible steady states of
 this form: $(p_n, p_i, m_n, 0)$ and $(p_n, p_i, 0, m_i)$. If the host is minimally facultative, i.e., r_p is low,
 these steady states exist if and only if the symbionts are beneficial,

$$Q_{p_{ij}} > 0 \quad \text{for } i \in \{1, 2\} \quad \text{and } j \neq i$$

and competition between hosts is weak,

$$c_p \leq \mu_p \min \left(1, \frac{Q_{p_{ij}}}{Q_p}, \frac{Q_p}{Q_{p_{ij}}}, \frac{Q_p Q_m + Q_{p_{ij}} Q_{m_{ji}}}{Q_p Q_{m_{ji}} + Q_{p_{ij}} Q_m} \right).$$

1278 Thus, the inclusion steady state with two hosts and one symbiont exists if **competition between**
 1279 **hosts is weak** and the remaining symbiont is beneficial.

We can compute the Jacobian matrix to explore the stability of this steady state. Let us
 look at the inclusion of the invasive host p_i by the native host p_n and its symbiont m_n , which
 corresponds to the steady state $(p_1^*, p_2^*, m_1^*, 0)$. The Jacobian is given by the following matrix

$$J(p_1, p_2, m_1, 0) = \left(\frac{J(p_1^*, p_2^*, m_1^*)}{0} \middle| \frac{B}{C} \right) \quad \text{where } C = Q_{m_{21}} \frac{p_1^*}{S} + Q_m \frac{p_2^*}{S} - c_m m_1^*.$$

1280 The eigenvalues of the matrix $J(p_1^*, m_1^*, m_2^*)$ are negative if the competition between the
 1281 symbionts is not too strong. In this case, the steady state is stable if and only if $C < 0$, which
 1282 is equivalent to

$$1283 \quad (Q_{m_{21}} \quad Q_m) \frac{C_p^{-1} \begin{pmatrix} Q_p \\ Q_{p_{21}} \end{pmatrix}}{S} < c_m. \quad (38)$$

1284 We consider now the two separate cases of strong and weak competition between symbionts.

1285 **Strong competition between symbionts.** If competition between symbionts is strong, i.e.,
 1286 c_m satisfies (38), this steady state is stable when it exists.

1287 **Weak competition between symbionts.** If, on the other hand, the competition between
 1288 symbionts is weak, this steady state is unstable.

1289
 1290 In sum, this steady state requires a beneficial symbiont (scenarios with a +), and weak
 1291 competition between hosts in conjunction with strong competition between symbionts.

1292 I.1.4 Coexistence steady state consisting of two hosts and two symbionts

1293 Here, we look at the special case when the native and the invasive symbionts are identical in
 1294 the sense that they are both harmful (scenario $(-, -)$), or both neutral (scenario $(0, 0)$), or
 1295 both beneficial (scenario $(+, +)$).

1296 In this case, the interaction matrices are symmetric that is $Q_{p12} = Q_{p21} = Q'_p$ and $Q_{m12} =$
 1297 $Q_{m21} = Q'_m$, where Q'_p and Q'_m satisfies properties (34). Thus, the coexistence steady state
 1298 takes the form (p^*, p^*, m^*, m^*) , because the matrices \mathbf{C}_p and \mathbf{C}_m are also symmetric, and it
 1299 satisfies

$$1300 \quad p^* = p_0 \frac{\mu_p}{\mu_p + c_p} + \frac{(Q_p + Q'_p)(Q_m + Q'_m)}{\frac{S_2}{d} + \frac{Q_m + Q'_m}{\mu_m + c_m}} \quad \text{and} \quad m^* = \frac{d(Q_m + Q'_m)}{\mu_m + c_m} \frac{\frac{S_2}{d}}{\frac{S_2}{d} + \frac{Q_m + Q'_m}{\mu_m + c_m}}, \quad (39)$$

where

$$S_2 = \frac{\tilde{p}_0}{2d} + \sqrt{\left(\frac{\tilde{p}_0}{2d}\right)^2 + p_0 \frac{Q_m + Q'_m}{\mu_m + c_m} + \frac{(Q_p + Q'_p)(Q_m + Q'_m)}{(\mu_m + c_m)(\mu_p + c_p)}} \quad \text{and} \quad \tilde{p}_0 = p_0 \frac{\mu_p}{\mu_p + c_p}.$$

1301 Even in the neutral scenario $(0, 0)$, where $Q'_p = 0$ and $Q'_m = 0$, the value of the coexistence
 1302 steady state depends on competition between both hosts and symbionts, thus it is different
 1303 from the exclusion steady state which does not depend on c .

The coexistence steady state always exists in the beneficial scenario $(+, +)$ and the neutral
 scenario $(0, 0)$. However, in the harmful scenario $(-, -)$, the coexistence exists only if the
 symbionts are not too harmful in the sense that $Q'_p = -q_p$ satisfies the following inequality

$$q_p \leq Q_p + r_p + \left(\frac{r_p}{2d}\right)^2 \frac{1}{\mu_p + c_p} \frac{\mu_m + c_m}{Q_m + q_m}.$$

Let us now look at the stability of the coexistence steady state in the three scenarios. We
 can compute the Jacobian around this steady state using the expression of section H.2:

$$J = \begin{pmatrix} J_p & B \\ C & J_m \end{pmatrix} \quad \text{where} \quad \begin{aligned} J_m &= -\mathbf{m} \cdot \left(\frac{\mathbf{Q}_m \mathbf{P}}{S^2} + \mathbf{C}_m \right) < 0 \\ B &= \frac{\mathbf{P}}{S^2} \cdot (S \mathbf{Q}_p - \mathbf{Q}_p \mathbf{m}) \\ C &= \frac{\mathbf{m}}{S^2} \cdot \left(S \mathbf{Q}_m - \frac{1}{d} \mathbf{Q}_m \mathbf{P} \right) \\ J_p &= -\mathbf{p} \cdot \left(\frac{\mathbf{Q}_p \mathbf{m}}{S^2} + \mathbf{C}_p \right) < 0. \end{aligned}$$

In our special case, the matrices J_p , J_m , B and C are symmetric and commute with each

other because they can be decomposed over the identity matrix I and the matrix of ones $\mathbf{1}$:

$$\begin{aligned}
J_p &= x_p I + y_p \mathbf{1} \quad \text{with} \quad x_p = -p^*(\mu_p - c_p) \quad y_p = -p^* \left(\frac{Q_p + Q'_p}{S^2} m^* + c_p \right) \\
J_m &= x_m I + y_m \mathbf{1} \quad \text{with} \quad x_m = -m^*(\mu_m - c_m) \quad y_m = -m^* \left(\frac{Q_m + Q'_m}{S^2} p^* + c_m \right) \\
B &= x_b I + y_b \mathbf{1} \quad \text{with} \quad x_b = \frac{p^*}{S} (Q_p - Q'_p) \quad y_b = \frac{p^*}{S^2} (S Q'_p - (Q_p + Q'_p) m^*) \\
C &= x_c I + y_c \mathbf{1} \quad \text{with} \quad x_c = \frac{m^*}{S} (Q_m - Q'_m) \quad y_c = \frac{m^*}{S^2} (S Q'_m - (Q_m + Q'_m) p^*) .
\end{aligned}$$

1304 Thus the eigenvalue of J are the roots of the following polynomial

$$\begin{aligned}
&\det((J_p - \lambda I)(J_m - \lambda I) - BC) \\
&= \det\left(\left((x_p - \lambda)(x_m - \lambda) - x_b x_c\right)I + \left((x_p - \lambda)y_m + (x_m - \lambda)y_p + 2y_m y_p - y_b x_c - y_c x_b - 2y_b y_c\right)\mathbf{1}\right) \\
1305 &= \left((x_p - \lambda)(x_m - \lambda) - x_b x_c\right)\left(\left((x_p - \lambda)(x_m - \lambda) - x_b x_c\right) + 2\left((x_p - \lambda)y_m + (x_m - \lambda)y_p\right.\right. \\
&\quad \left.\left.+ 2y_m y_p - y_b x_c - y_c x_b - 2y_b y_c\right)\right) .
\end{aligned}$$

1306 Thus, two of the eigenvalues are roots of the following polynomial

$$1307 \quad \lambda^2 - (x_p + x_m)\lambda + x_p x_m - x_b x_c = 0 . \quad (40)$$

1308 **Strong competition between hosts and between symbionts.** If competition between
1309 hosts and between symbionts is strong, that is $c_p > \mu_p$ and $c_m > \mu_m$ then the coexistence
1310 steady state is unstable for any scenarios: harmful $(-, -)$, neutral $(0, 0)$ or beneficial $(+, +)$.
1311 Indeed in this case, the polynomial (40) has always a negative root.

1312 **Weak competition between hosts and symbionts.** Conversely, when the competition is
1313 weak between both the hosts and the symbionts, that is $c_p < \mu_p$ and $c_m < \mu_m$, then the
1314 coexistence state might be stable. Indeed, the eigenvalue are all negative in this case.

1315 **Mixed competition (weak/strong).** Now, if competition between hosts is strong while
1316 competition between symbionts is weak (or viceversa), then the coexistence steady state is
1317 unstable when the symbionts are either beneficial (scenario $(+, +)$) or neutral (scenario $(0, 0)$).
1318 However, when the symbionts are harmful to their new host (scenario $(-, -)$), the coexistence
1319 steady state might be stable if one competitor is much stronger than the other.

1320 I.2 Outcomes of the different interaction scenarios

1321 In this section we discuss the different interaction scenarios presented in Fig. 3. We investigate
1322 the possible stable steady states of the system consisting of a native host and its symbionts,
1323 interacting with an invasive and its symbionts for different degrees of competition between
1324 hosts and between symbionts, and for different degrees of facultative mutualism.

1325 I.2.1 Neutral symbionts $(0, 0)$

1326 In this case, the only possible steady states are the two exclusion states $(p_n^*, 0, m_n^*, 0)$ and
1327 $(0, p_i^*, 0, m_i^*)$, the inclusion steady state consisting of two plants and a symbiont $(p_n^*, p_i^*, m_n^*, 0)$
1328 and $(p_n^*, p_i^*, 0, m_i^*)$ or the coexistence state $(p_n^*, p_i^*, m_n^*, m_i^*)$.

Weak competition between hosts and between symbionts. If competition between hosts is weak in the sense that

$$c_p \leq \mu_p \left(1 - \frac{1}{S^2} \frac{Q_p Q_m}{\mu_p \mu_m} \right), \quad \text{where } S = \frac{p_0}{2d} + \sqrt{\left(\frac{p_0}{2d} \right)^2 + p_0 \frac{Q_m}{\mu_m} + \frac{Q_m Q_p}{\mu_m \mu_p}},$$

1329 and the competition between symbiont is also weak,

$$1330 \quad c_m \leq \mu_m \left(1 - \frac{Q_m Q_p}{\mu_m (\mu_p - c_p)} \right). \quad (41)$$

1331 then coexistence occurs.

1332 **Strong competition between hosts or strong competition between symbionts.** When
1333 competition between hosts or between symbionts is strong, and the hosts are obligate mu-
1334 tualists, then competitive exclusion of one of the two hosts/symbionts, and successively of
1335 its associated symbiont/host, occurs. If the host is a facultative mutualist, then the scenario
1336 described below can occur.

1337 **Weak competition between hosts and strong competition between symbionts.** If com-
1338 petition between symbionts is strong, while the competition between hosts is weak, steady
1339 state stability depends on the degree of mutualism of the host (whether obligate or facultative).
1340 If the plant is an obligate mutualist, strong competition between the symbionts will
1341 cause one of the two symbionts to be competitively excluded. The associated host will then
1342 consequently go extinct. Therefore, in this case, only the exclusion steady state consisting of
1343 native host and their symbionts or of invasive hosts and their symbionts are possible. If the
1344 hosts are facultative mutualists, then the inclusion steady state consisting of two plants and a
1345 symbiont can occur, where one host survives in the absence of the symbiont, while the other
1346 persists in combination with its associated symbiont.

1347 **I.2.2 A harmful symbiont versus a beneficial symbiont $(-, +)$ and $(+, -)$**

1348 Without loss of generality, we can consider the situation in which the invasive symbiont is
1349 harmful to the native host while the native symbiont is beneficial to the invasive host, that
1350 is scenario $(-, +)$. In this situation, we expect the invasive host with its symbiont to replace
1351 the native host and either to integrate or to exclude the native symbiont.

1352 Indeed in this scenario, considering that the host is an obligate or weakly facultative
1353 mutualist, and that a harmful symbiont is harmful enough to not allow host growth in its
1354 presence (as considered in our parameter choice of Table 1), the possible steady state are: the
1355 exclusion steady state composed of the invasive host and its invasive symbiont $(0, 0, p_i^*, m_i^*)$,
1356 the exclusion steady state composed of the invasive host and the native symbiont $(0, m_n^*, p_i^*, 0)$,
1357 or the inclusion of the native symbiont into the invasive host-symbiont pair $(0, p_i^*, m_n^*, m_i^*)$.
1358 Even when other steady states might exist, they are barely stable and very unlikely to persist.

1359 **Weak competition between symbionts.** If the competition between symbionts is weak,
1360 that is $c_m \leq \mu_m$, then native and invasive symbionts will coexist $(0, m_n^*, p_i^*, m_i^*)$, thus the
1361 native symbionts is included in the invasive community of symbionts.

Strong competition between symbionts. If competition between symbionts is strong, that is $c_m > \mu_m$, then the symbionts will exclude each other. Thanks to the advantage of the invasive symbiont, which is harmful to the native host, the invasive species will generally exclude the native species $(0, 0, p_i^*, m_i^*)$. However, strong asymmetric competition favoring the native symbiont (i.e., when $c_{mni} \gg c_{min}$) can lead to stability of the steady state $(0, m_n^*, p_i^*, 0)$.

Strong facultative hosts with weak competition between them. When the host is strongly facultative, that is its intrinsic growth rate is high compared with the exchange rates Q_p , then different outcomes may occur. Under this assumption, new possible steady states exist: the inclusion of the native host in the invasive pair $(p_n^*, 0, p_i^*, m_i^*)$ and the coexistence state $(p_n^*, m_n^*, p_i^*, m_i^*)$.

If competition between hosts is weak in the sense that

$$c_p \leq \frac{\mu_p Q_p - q_p}{2 Q_p} \quad (42)$$

then the hosts will coexist. If competition between symbionts is weak, that is

$$c_m \leq \frac{Q_m Q_p - q_p}{S \mu_p + c_p}, \quad (43)$$

then native and invasive hosts and symbionts will coexist $(p_n^*, p_i^*, m_n^*, m_i^*)$. Otherwise, if competition between symbionts is strong $c_m \geq \mu_m$, then the native symbionts is replaced by the invasive symbiont while native and invasive hosts coexist $(p_n^*, p_i^*, 0, m_i^*)$.

If competition between hosts is strong, that is $c_p > \mu_p$, then hosts can not coexist, and we recover the previous results discussed above, for the case in which hosts are poor facultative mutualists.

1.2.3 A harmful symbiont versus a neutral symbiont $(-, 0)$ and $(0, -)$

In this scenarios, if we consider that the harmful symbiont is harmful enough to not allow for host growth in its presence, only the exclusion steady states $(p_n^*, m_n^*, 0, 0)$ and $(0, 0, p_i^*, m_i^*)$ exist. Because one symbiont is harmful and the other is neutral, mixed host-symbiont combinations do not exist if the hosts are poor facultative mutualists. When hosts are strong facultative mutualists, this steady state is always unstable as soon as competition between hosts is not too weak, that is $c_p \geq \mu_p - (Q_p + q_p)Q_m/(\mu_m S^2)$.

In addition, the pair with the neutral symbiont is also unstable if competition between symbionts is not too strong that is

$$c_m < \frac{q_m}{Q_m} \mu_m, \quad \text{where } q_m > Q_m.$$

Thus, in scenario $(-, 0)$ the invasive steady state $(0, 0, p_i^*, m_i^*)$ is always stable (see Fig. A.2) while in the scenario $(0, -)$, the native steady state $(p_n^*, m_n^*, 0, 0)$ is always stable (see Fig. A.2). When the harmful symbiont is only weakly parasitic to the new host, and competition between hosts or between symbionts is weak, hosts and symbionts may coexist.

1.2.4 A beneficial symbiont versus a neutral symbiont $(+, 0)$ and $(0, +)$

In this scenario, we expect a diversity of outcomes depending on the strength of competition between the species.

1396 **Strong competition between hosts and symbionts** If competition between hosts and
 1397 between symbionts is strong, that is $c_p \geq \mu_p$ and $c_m \geq \mu_m$, only the exclusion steady states
 1398 $(p_n^*, m_n^*, 0, 0)$, $(0, 0, p_i^*, m_i^*)$, $(p_n^*, 0, 0, m_i^*)$ and $(0, m_n^*, p_i^*, 0)$ exist and are stable. In this case,
 1399 when competition between invasive and native hosts and symbionts is symmetric and equal in
 1400 both directions, the outcome of the interaction truly depends on the initial quantity of each
 1401 species. In particular, species that are more abundant than others are more likely to persist.
 1402 However, if host and symbionts have similar initial biomass then the invasive symbiont will
 1403 replace the native symbionts and the native host will exclude the invasive host.

1404 **Weak competition between hosts and symbionts** As soon as competition between hosts
 1405 and symbionts is weak, that is $c_p \leq \mu_p$ and $c_m \leq \mu_m$, the exclusion steady states are unstable.
 1406 If the competition is weak enough, that is c_p and c_m satisfies conditions (33) the coexistence
 1407 steady state exist and it is stable. In this case, the invasive species would coexist with natives.

1408 **Mixed competition (strong/weak)** If competition between hosts is strong while compe-
 1409 tition between symbionts is weak (or if competition between hosts is weak while competition
 1410 between symbionts is strong), the inclusion steady states made of two hosts and one symbionts
 1411 (or one host and two symbionts) occur and are stable. More precisely, if the competition be-
 1412 tween hosts is strong, that is $c_p \geq \mu_p$, while competition between symbionts is weak, that is
 1413 $c_m \leq \mu_m$, then the native host includes the invasive symbiont in its community because the
 1414 steady state $(p_n^*, 0, m_n^*, m_i^*)$ is stable (see section I.1.2 and Fig. A.2).

1415 Conversely, if the competition between hosts is weak, that is $c_p \leq \mu_p$, while competition
 1416 between symbionts is strong, that is $c_m > \frac{\mu_m}{2}$, then the native symbiont exclude the invasive
 1417 symbiont and the native symbiont support the native and the invasive host because the steady
 1418 state $(p_n^*, p_i^*, m_n^*, 0)$ is stable (see section I.1.3 and Fig. A.2).

1419 I.2.5 Similar symbionts (+, +), (-, -)

1420 In this scenario, we assume that the native and invasive symbionts are either harmful (-, -)
 1421 or beneficial (+, +) to their hosts.

1422 **Strong competition between hosts and symbionts** In this case, the only possible steady
 1423 states are the exclusion steady states $(p_n^*, m_n^*, 0, 0)$, $(0, 0, p_i^*, m_i^*)$, $(p_n^*, 0, 0, m_i^*)$ and $(0, m_n^*, p_i^*, 0)$.
 1424 When species are similar, the outcome of the interaction only depends on the initial condi-
 1425 tions. If the symbionts are harmful, only the native or the invasive species will survive. While
 1426 if the symbionts are beneficial, the native host and/or the native symbiont can be replaced.

1427 **Weak competition between hosts and symbionts** If competition between hosts and sym-
 1428 bionts is weak, then the coexistence steady state exists and it is stable (see Fig. A.2).

1429 **Mixed competition (weak/strong) with beneficial symbionts (+, +)** If either the compe-
 1430 tition between hosts or between symbionts is strong, then the coexistence steady state
 1431 cannot occur, because either the hosts exclude each other or the symbionts exclude each
 1432 other. However, if one of the competition is weak, the steady states consisting of one hosts
 1433 and two symbionts, or of one symbiont and two hosts are stable.

1434 In particular, if the competition between hosts is strong, that is $c_p \geq \mu_p$, and competition
 1435 between symbionts is weak, that is $c_m < \mu_m$ then the steady states $(p_n^*, 0, m_n^*, m_i^*)$ and
 1436 $(0, p_i^*, m_n^*, m_i^*)$ are stable. Depending on the initial conditions, the native host will include

1437 the invasive symbiont in its community and exclude the invasive host, or the invasive host
1438 will replace the native host and includes the native symbiont in its community.

1439 Conversely, if the competition between hosts is weak, that is $c_p \leq \mu_p$, and competition
1440 between symbionts is strong, that is $c_m > \mu_m$, then the steady states $(p_n^*, p_i^*, m_n^*, 0)$ and
1441 $(p_n^*, p_i^*, 0, m_i^*)$ are stable. Depending on the initial conditions, the native symbiont will exclude
1442 the invasive host or the invasive host will exclude the native.

1443 **Mixed competition (strong/weak) with harmful symbionts** $(-, -)$ Now let us assume
1444 that the symbionts are harmful $(-, -)$ and the competition between either hosts or symbionts
1445 is strong, that is either $c_p \geq \mu_p$ or $c_m \geq \mu_m$. In this case, even if the competition between hosts
1446 or between symbionts is strong, the coexistence steady state remains stable if the competition
1447 is not too strong, as long as the the following inequality holds true

$$1448 \quad -(\mu_p - c_p)(\mu_m - c_m) \leq (q_m - Q_m)(Q_p + q_p)$$

1449 (see stability analysis in section I.1.4 for more details).