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.
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- Interactive reproduction and re-parametrization of results can also be done through the modelRxiv platform (`https://modelrxiv.org/model/YfndNX`).

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Abstract

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, microbially mediated, linked invasion, mathematical model, differential equation, host-symbiont, mutualism, invasion, microbial invasion, plant invasion, theoretical framework.

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 facilitate the establishment of an introduced host population and its expansion into a new range (Dawkins and Esiobu, 2016; Parepa et al., 2013; Moeller et al., 2015). Analogously, the spillover of parasites or pathogens from invasive to native hosts can weaken a native population, and eventually lead to its extinction (Panzavolta et al., 2021; Santini et al., 2013; Grünwald et al., 2012; Schuchert et al., 2014). Microbially mediated effects can also provide resilience to native communities. For instance, host invasiveness may be decreased by a

reduction in the abundance of invasive symbionts (Zenni and Nuñez, 2013; Catford et al., 2009), or by the transmission of pathogenic agents from native to invasive hosts (Mordecai, 2013; Flory and Clay, 2013).

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

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

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.

ing the necessary simplicity to allow analytical tractability, is key to providing a predictive understanding of the dynamics of host-microbial communities and their invasibility.

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

Despite their opposite effects on host fitness, invasion dynamics driven by beneficial microbes or harmful microbes may present similar interaction motifs (Dickie et al., 2017). For instance, the formation of mutualistic associations between invasive hosts and native mycorrhizal fungi (i.e., an association that would benefit invasive hosts) and the transmission of invasive pathogens to native hosts (i.e., an association that may weaken native hosts) may lead to similar outputs, namely providing a competitive advantage to invasive hosts and increasing their invasion success. Our model characterization allows us to identify and organize these unifying patterns of microbially mediated invasion through the exploration, within a single framework, of dynamics occurring when microbial influence on host growth may range from beneficial to harmful, depending on the balance between the benefits and costs of the association.

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

2 Model and Methods

2.1 Mathematical framework

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

and invasive microbes may exchange resources with native hosts. Competition between native and invasive hosts (c_p parameters) and between native and invasive symbionts (c_m parameters), may reduce their abundance, e.g., due to competition for host colonization between microbes (Engelmoer et al., 2014; Smith et al., 2018), or due to host competition for light or other external resources (Craine and Dybzinski, 2013).

We obtain the following equations:

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

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

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

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

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

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

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

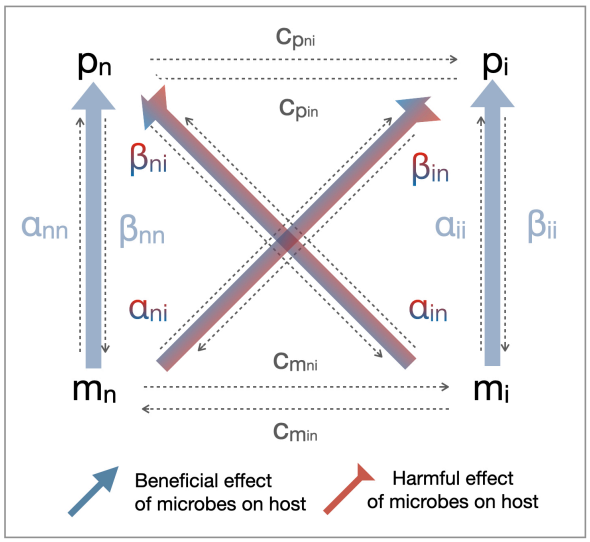


Fig. 1: Schematic representation of the model of Eq. (1). A native microbial community m_n is associated with a host population p_n. Resource exchange between hosts and microbes is quantified by parameters α_{nn} (microbes to hosts) and β_{nn} (hosts to microbes). Similarly, a population of invasive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

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

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

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

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

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

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

2.2 Harmful and beneficial microbes

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

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

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

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

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

$$\frac{q_{cp}}{q_{hp}} \beta_{in}\, d < \alpha_{ni}^* < \alpha_{ii} \tag{6}$$

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

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

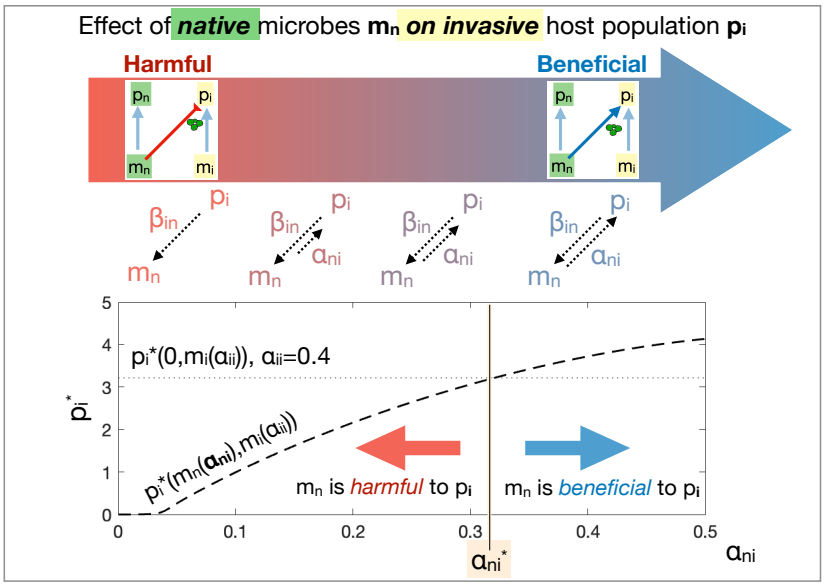


Fig. 2: The direct effect of a native microbial community m_n on an invasive host population may range from harmful (in red) to beneficial (in blue). We can explore this range by varying parameter α_{ni}, which quantifies the benefit provided by native microbes to invasive hosts, while all other parameters 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.

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 invasive hosts.

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

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

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

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

3 Results

3.1 Overview of interaction scenarios

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

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

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

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

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

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

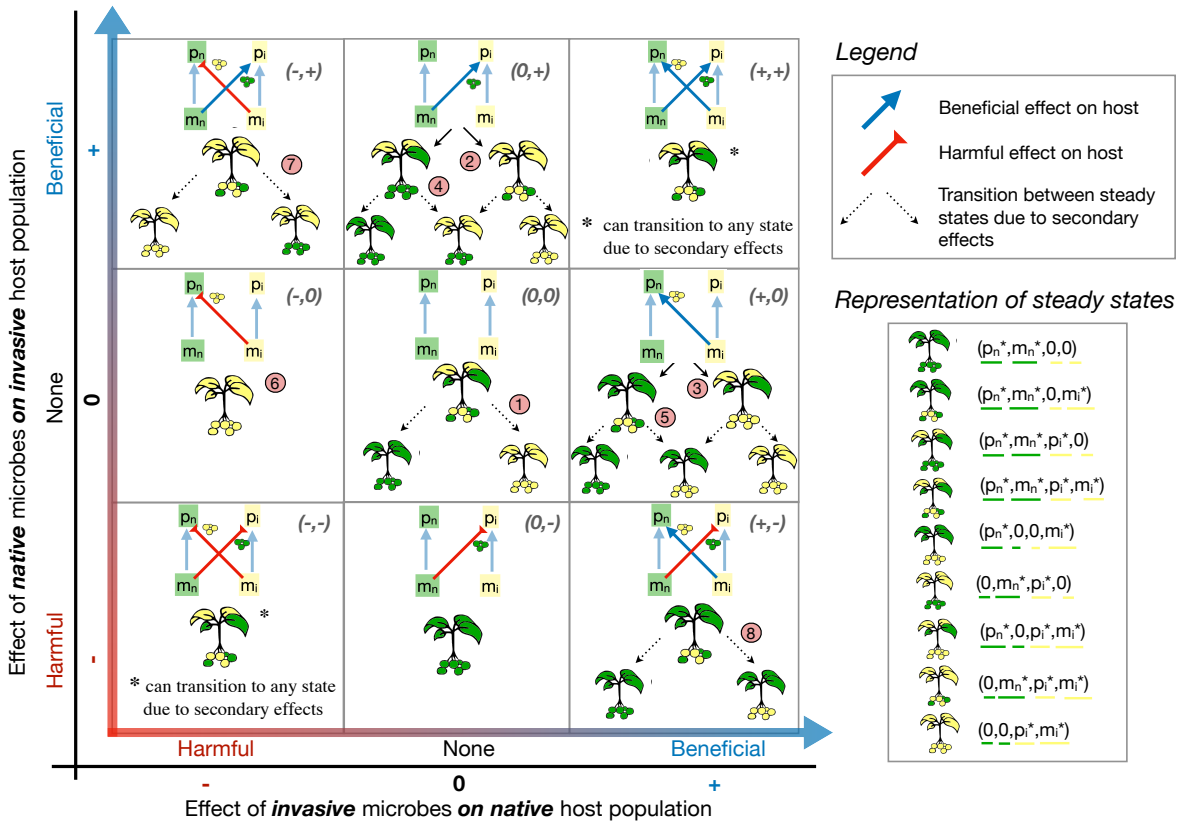


Fig. 3: Possible microbially mediated invasion dynamics occurring when native and invasive species share their beneficial or harmful microbes. The horizontal axis represents the effect of invasive microbes on native hosts (which can be harmful '−', neutral '0', or beneficial '+'), while the vertical 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`).

3.2 Dynamics of microbially mediated invasion

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

1 Co-invasion via no microbial sharing: When no microbial sharing occurs, competitive exclusion of one host-symbiont community, either the native or the invasive one, occurs through selection due to trait differences or differences in initial abundance, or through drift (not considered here). When selection due to trait differences occur, the host-microbial associations that provides the highest fitness to either hosts or symbionts outcompete the other. Highest fitness can be provided through 'secondary effects', such as differences in the competitive effect of one species on another, or differences in stress tolerance, as explained at the end

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

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

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

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

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

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

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

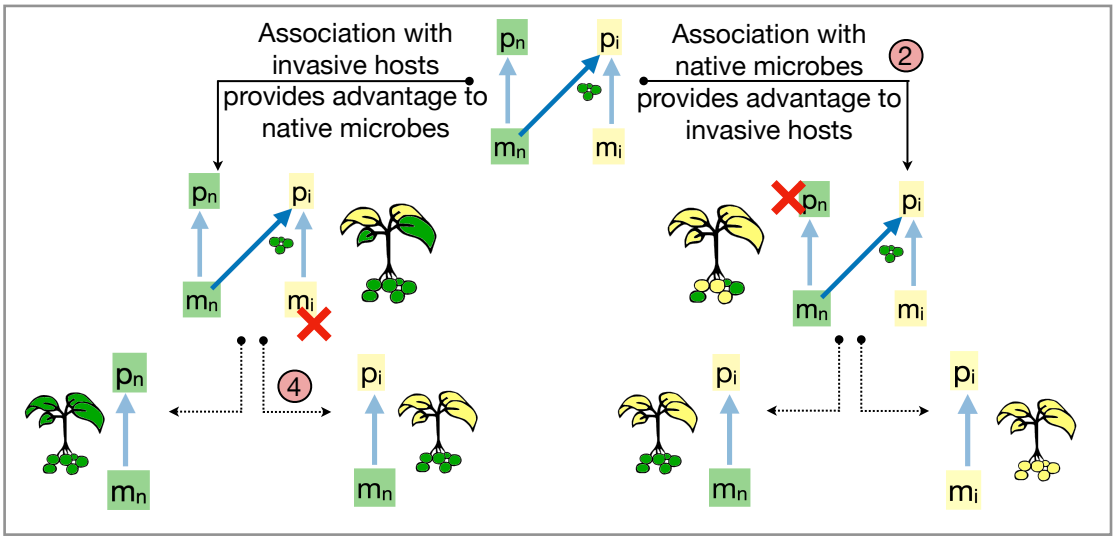
invasive symbionts (Fig. 4a, left pathway, and SI I.2.4 for details). Exclusion of invasive symbionts may provide a competitive advantage to invasive hosts, and lead to the exclusion of native hosts, particularly if invasive symbionts are low quality mutualists, or even parasitic to their host (see Fig.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

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

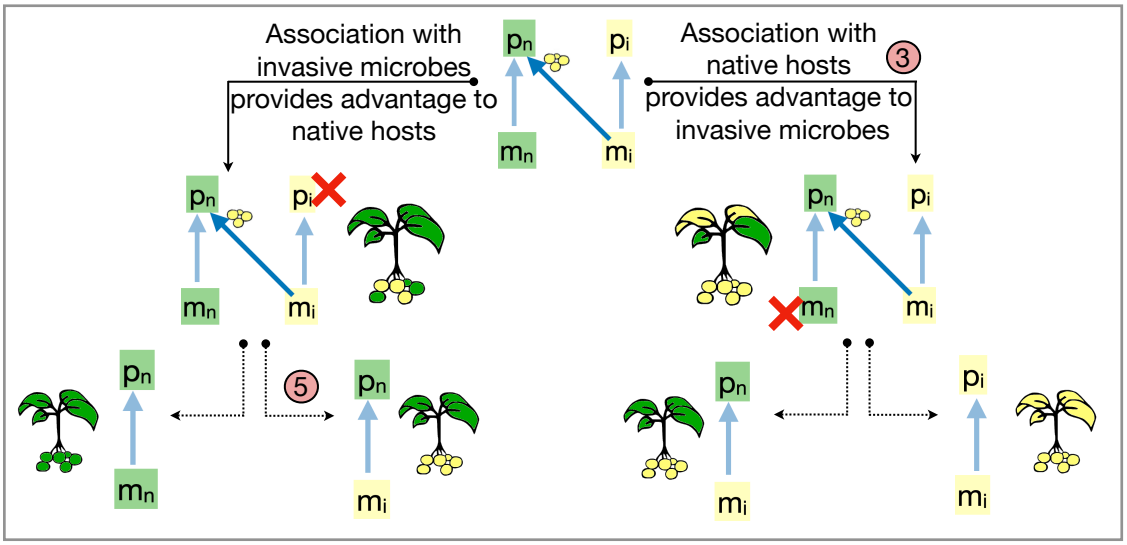
6 Co-invasion via spillover of harmful microbes: Co-invasion may be facilitated if invasive symbionts are harmful to native species, which would weaken native hosts and cause their competitive exclusion and the consequent exclusion of their symbionts (see SI I.2.3 for further insights). This situation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

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

8 Microbial invasion via spillback of harmful microbes and spillover of beneficial microbes: The dynamics of microbial invasion described in 5 is more likely to occur if 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.

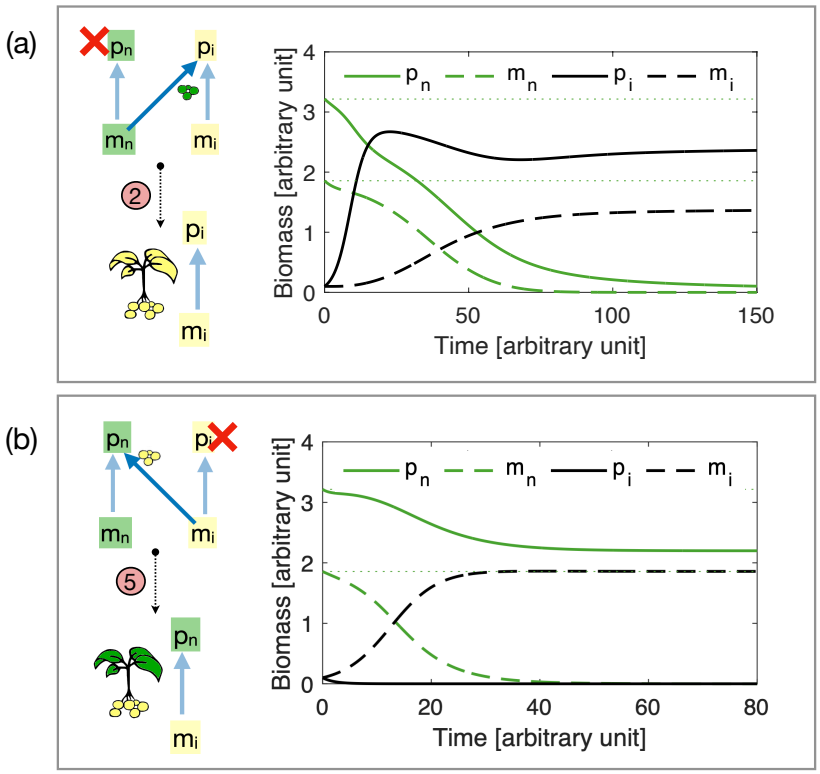


Fig. 5: (a) Possible dynamics of microbially mediated co-invasion occurring when native symbionts associate with less beneficial invasive hosts. These associations may lead to the indirect exploitation of native hosts, and to their competitive exclusion by invasive hosts. In turn, native symbionts may 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`).

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

4 Discussion

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

4.1 Microbially mediated increase in invasion risk

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

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

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

In some instances, microbially mediated invasion may lead to changes in total community biomass with, in some circumstances, long-term repercussions on ecosystem functionality (Nunez and Dickie, 2014; Lovett et al., 2006; Dickie et al., 2011; Mitchell and Power, 2003; Cobb and Rizzo, 2016; Preston et al., 2016; Ehrenfeld, 2010). Although this reduction in community biomass is well-known for pathogen spread (Lovett et al., 2006; Mitchell and Power, 2003; Cobb and Rizzo, 2016; Preston et al., 2016), here we present alternative mechanisms that can lead to an invasion-driven biomass decrease through higher-order interactions (Billick and Case, 1994; Mayfield and Stouffer, 2017). For example, if invasive hosts provide a reduced reward as compared to natives (Hoffman and Mitchell, 1986; Mummey and Rillig, 2006; Hausmann and Hawkes, 2009; Vogelsang and Bever, 2009), associations between invasive hosts and native symbionts will lead to the direct exploitation of the resources provided by native symbionts. In addition, there will be indirect exploitation of more mutualistic native hosts that invested resources in the growth of a large native microbial community from which it can no longer fully benefit. Thus, in this case, an increase in the abundance of invasive hosts occurs in conjunction with a decrease in the abundance of native symbionts and their 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; Dinoor 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; Prevéy and Seastedt, 2015). Other more complex dynamics of biotic resistance occur when native symbionts, which have co-evolved with native hosts, are highly mutualistic to native hosts but not to invasive hosts (Bunn et al., 2015; Moora et al., 2011). 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

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

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

5 Concluding remarks

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

Author's contributions

MMM: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing - Original Draft, Writing - Review & Editing. JG: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Review & Editing. RT: Conceptualization, Methodology, Writing - Review & Editing. KH: Results visualization on modelRxiv. OK: Conceptualization, Methodology, Writing - Review & Editing.

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