Beyond timescale separation: An eco-evolutionary consumer-resource theory of host-microbe symbioses

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January 28, 2026

Abstract

Symbiotic associations between microorganisms and hosts are universal and dynamic. However, current ecological and evolutionary theory often simplistically analyzes hosts and symbionts as either separate or fully integrated entities. This entrenchment obscures a central research challenge: to understand symbioses across varying degrees of interaction, integration, and functional dependence. We posit that major advances will emerge from theoretical models that explicitly capture eco-evolutionary feedbacks linking host and microbial community interaction structure, biotic resource availability, and selection across biological levels. We show how extending consumer-resource theory to incorporate evolutionary processes can overcome limitations in separation of timescales approaches, advancing our understanding of the evolution, adaptability, and persistence of variable host-microbe symbioses. By coupling ecological and evolutionary dynamics across scales, this framework can guide both basic understanding and applied approaches in symbiosis research.

Keywords : host-microbiome, mutualism, cooperation, multi-level selection, holobiont, hologenome, mathematical models, consumer-resource, eco-evolutionary, host-microbe interactions

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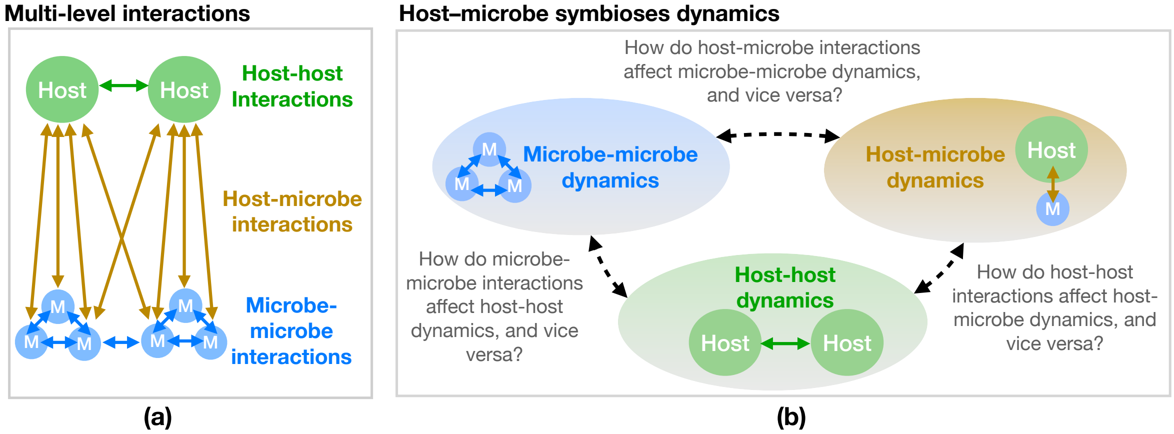
Overview

Host-microbe symbioses are essential components of the biosphere, with profound ecological and economic significance. Canonical interactions involve eukaryotic hosts associating with a multitude of microbial species. Examples span beneficial plant-fungal interactions that hold promise for sustainable agriculture and forestry (Mora et al., 2023), coral-reef ecosystems that are integral to the economic and environmental sustainability of tropical communities (Thompson et al., 2015), and the human gut and its symbiotic microbiome which together shape host metabolism and the balance between health and disease (Lozupone et al., 2012). Despite their importance, our understanding of the mechanisms underlying the emergence, stability, and evolution of symbioses remains limited and overly simplified (Araujo et al., 2024; Koskella et al., 2017; Ferretti et al., 2025; Week et al., 2025; Bordenstein, 2024).

The evolutionary and population dynamics of host-microbe symbioses can differ fundamentally from those of their component single species, due to emergent properties arising from species interactions. Symbioses encompass multiple interacting partners that vary in their degree of functional and physiological integration, interdependence (obligate to facultative), inheritance mode (vertical to horizontal), interaction outcome (beneficial to harmful), evolutionary rates, and reproductive cycles. All of these processes operate simultaneously and influence one another across timescales. For example, host physiological responses, behaviour, and social structure shape microbiome acquisition and persistence (Ross et al., 2024; Sarkar et al., 2024; Mazel et al., 2025; Aspenberg et al., 2023), and microbial generation times and ecological dynamics can rapidly feed back on host traits, driving evolutionary change (Henry et al., 2021; Kolodny and Schulenburg, 2020; Brooks et al., 2016). This holistic perspective on symbioses emphasizes how biological form and function emerges within diverse symbiotic associations (Bordenstein, 2024). We contend that these emergent properties can be tractably modeled using modified consumer-resource modeling frameworks.

Theoretical advancements offer a path to clarify how host-microbe interactions and their interdependence influence host and microbial growth and evolution. Yet modeling symbioses remains challenging, as theoretical treatment must address their intricate hierarchical nature (Fig. 1a). Microbial communities within hosts can encompass hundreds of microbial species, each of which may in turn hosts its own symbionts, such as viruses and other mobile genetic elements (Hum, 2012; Lang et al., 2025). Interactions between hosts and among microbes –both within and across hosts– generate population processes that span multiple ecological and evolutionary dimensions and timescales, often involving inherent conflicts of interest (Van Baalen and Jansen, 2001; Figueiredo and Kramer, 2020; Richards and Moran, 2024; Malagon et al., 2025). Inheritance modes further influence evolutionary trajectories by aligning or decoupling host and symbiont fitness (Fisher et al., 2017; Bull et al., 1991; Akçay, 2015). It therefore remains unclear how this interplay of divergent forces ultimately determines host and microbial evolution and community structure (Fig. 1b).

Existing theoretical frameworks each capture elements of host-symbiont dynamics but remain limited in their ability to provide a comprehensive theory. We posit that a useful starting point to develop this theory is to view symbioses –literally 'living together'– as systems in which partners serve as one another's biotic environment and influence the availability of resources within it. We introduce an eco-evolutionary consumer-resource framework that brings together and extends previous theoretical approaches, providing a unified tool to study host-microbe symbioses. Such a framework enables tracking of multiple interacting and evolving populations linked through shared resources and selective forces, operating at comparable timescales. By coupling ecological and evolutionary processes, this approach reveals alternative pathways shaping the resilience, productivity, adaptability, and potential collapse of symbioses.


Multi-level interactions

Host–microbe symbioses dynamics

How do host-microbe interactions affect microbe-microbe dynamics, and vice versa?

How do microbe-microbe interactions affect host-host dynamics, and vice versa?

How do host-host interactions affect host-microbe dynamics, and vice versa?

Fig. 1: Host-microbe symbioses are multi-level dynamical systems. (a) A schematic representation of multi-level population structure and dynamics characteristic of host-microbe symbioses. (b) Interactions among hosts, between hosts and microbes, and among microbes can influence one another, collectively shaping the population and evolutionary dynamics of host-microbe symbioses.

When consumers are also resource providers

The mathematical formalism we develop below sits on a simple conceptual framing: the resource landscape of the host is shaped (positively and negatively) by its symbionts, and concurrently the symbiont resource landscape is shaped by its host. For example, host-derived substances such as mucus and other organic compounds can influence microbial growth and survival (Bergstrom and Xia, 2022; Quinn et al., 2024), whereas microbes can supply hosts with diverse metabolites that can help or harm host survival and growth (Feng et al., 2019; Salem et al., 2014). In this way, host-microbe interactions influence not only community structure, but also the availability of biotic resources. This framing suggests that host-microbe symbioses can be naturally modeled as reciprocal consumer-resource dynamics.

Consumer-resource models of mutualism provide a theoretical basis for understanding which dynamics are produced when processes of resource acquisition and provision translate into biomass densities of the interacting species (Holland and DeAngelis, 2010). Despite the name, these models are not limited to the study of mutualistic interactions. Reciprocal influences can be uni- or bidirectional and range along a continuum from mutually beneficial to mutually harmful, depending on the cost and benefit of each interaction. The functional forms of resource exchange, both benefits and costs, can be linear or saturating, or empirically grounded in more complex relationships that reflect how host- or microbe-associated resource availability and biomass conversion depend on the densities of interacting species (Holland et al., 2002; Walmsley et al., 2025). This formalism explicitly couples host and microbial dynamics, reflecting the conceptual view of hosts and microbes as reciprocal consumers of each other's resources, while implicitly accounting for chemical intermediates and their dependence on biomass densities through the benefit and cost functions. Such consumer-resource models can capture a wide spectrum of outcomes, many of which remain unexplored.

To date, consumer-resource models of mutualism have primarily focused on two-species systems (Fig. 2a), examining the conditions for ecological stability of mutually beneficial relationships (Hale and Valdovinos, 2021; Holland, 2015; Osuna et al., 2025). Extensions of these models to larger, multi-species communities demonstrate how the interplay between host-microbe dynamics, which govern resource flows, and community-level ecological dynamics, which shape resource-driven selection, can generate outcomes not predicted by simpler pairwise or single-population models (see Fig. 2c, which accounts for the processes shown in

2a and 2b). These models can provide insights into the maintenance of microbial diversity that are specific to host-microbe symbioses (Bachelot and Lee, 2018; Martignoni et al., 2020a; Valdovinos, 2019). For example, they show how microbial competitors can coexist through key mediator species that enhance host-provided resources (Martignoni et al., 2020b; Narayanan et al., 2025). They also highlight that microbial interactions can be non-additive and context-dependent, with synergistic or antagonistic effects on host performance and disease outcomes (Rawstern et al., 2025; Afkhami et al., 2014). Furthermore, these models allow exploration of new ecological scenarios, such as symbiont-mediated invasion (Martignoni et al., 2025; Ladau et al., 2025; Dickie et al., 2017).

Despite these advances, consumer-resource models with fixed traits and interaction structures are constrained in their ability to explain how host-microbe associations originate and evolve. By treating symbiont traits and interaction types as static, these frameworks can characterize the ecological consequences of mutualistic or parasitic relationships, but cannot account for evolutionary transitions between them or for the emergence of mutualism itself. In host-microbe systems, selection pressures arise from ecological context –such as host density, competition, and resource availability– which in turn are shaped by host and symbiont traits. Capturing these reciprocal feedbacks requires explicitly incorporating evolution, allowing symbiont and host traits to respond to and reshape the ecological dynamics that generate selection. We discuss this further in the next section.

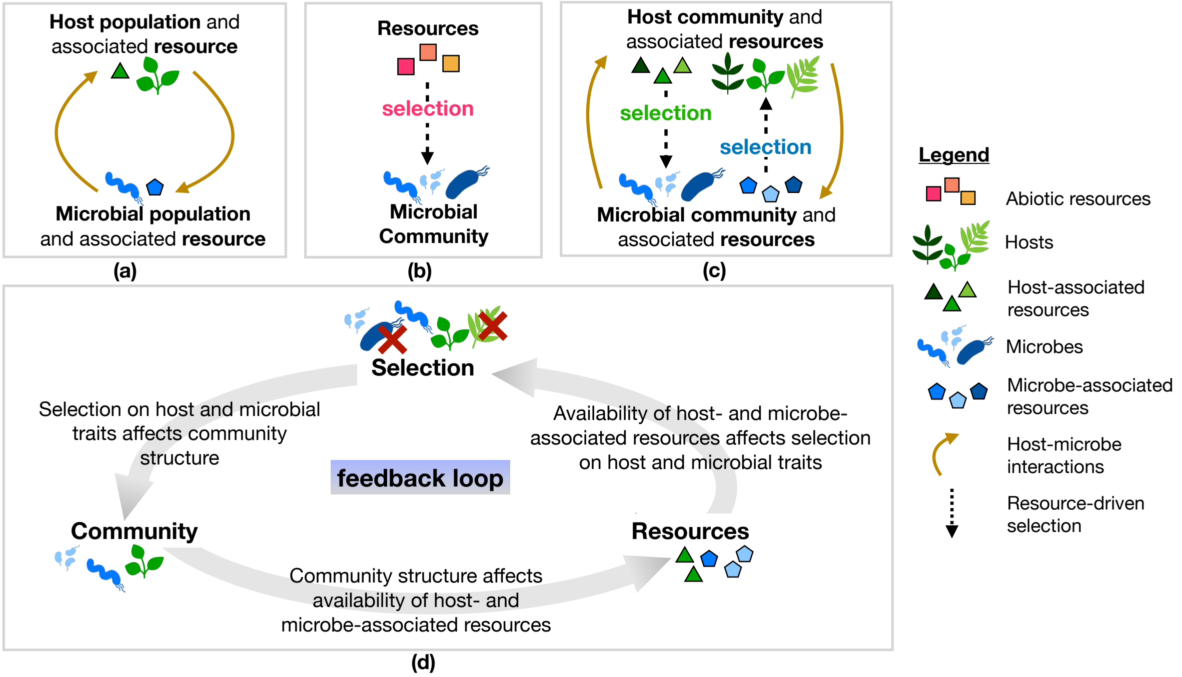


Fig. 2: Reciprocal resource exchange links partner traits to community dynamics and selection. (a) Consumer-resource interactions in which two parties (e.g., host and symbiont) simultaneously act as both consumer and resource-providers (Box 1, Eq. (1)). (b) Resource availability influences selection through the structure of ecological interactions. (c) The parties in case (a) are replaced by whole communities (e.g., microbial and host populations, see Box 1, Eqs. (2) and (3)). As a result, selection becomes possible and can shift community composition. Resource availability in one community (e.g., host-derived resources) affects selection in the other (e.g., by shaping microbial interaction dynamics, or by affecting the fitness of particular traits), and vice versa. (d) Example of a feedback loop captured by eco-evolutionary consumer-resource models. Selection shapes host and microbial community composition, community composition alters resource availability, and resource availability in turn modifies selection.

Box 1: Eco-evolutionary consumer-resource models

Consider multiple populations of interacting hosts and symbionts, denoted by H_i and M_j, for $i \in \{1, \dots, I\}$ and $j \in \{1, \dots, J\}$. Each population is structured into subpopulations characterized by host trait values x_k and microbial trait values y_s, with $k \in \{1, \dots, K\}$ and $s \in \{1, \dots, S\}$, such that

$$H_i = (h_i(x_1), \dots, h_i(x_K)) \quad \text{and} \quad M_j = (m_j(y_1), \dots, m_j(y_S)).$$

Traits quantify, for example, resource exchange capacity or symbiotic dependence, and may evolve through genetic or phenotypic variation, either at birth or throughout life. Changes in trait-structured host biomass $h_i(x_k)$ and microbial biomass $m_j(y_s)$ depend on:

- **Multi-level interactions**, as shown in Fig. 1a, and defined by:
    - host- and microbial-specific growth rates $f_{R_{h_i}}$ and $f_{R_{m_j}}$. These functions describe, respectively, **host-host interactions** and **microbe-microbe interactions**, and account for density- and trait-dependence in both growth and ecological interactions;
    - the total ***benefit*** and total ***cost*** of **host-microbe interaction**, through benefit functions $f_{B_{h_i \leftarrow M_j}}$ and $f_{B_{m_j \leftarrow H_i}}$, and cost functions $f_{C_{h_i \rightarrow M_j}}$ and $f_{C_{m_j \rightarrow h_i}}$. These functions describe the individual contributions of each host-microbe interaction, and can be modulated by host and microbe traits, and by the presence of other hosts and/or symbionts (e.g., if these are competing for the same shared resource).
- **Evolutionary processes**, described as **diversification** in host and/or microbial traits. Trait diversification occurs at rates σ_{h_i} and σ_{m_j}, with dynamics determined by diversification matrices $\mathbf{D}_{h_i}$ and $\mathbf{D}_{m_j}$, which satisfy $\mathbf{D}(z, z') \geq 0$ for $z \neq z'$ and $\mathbf{D}(z, z) = -\sum_{z' \neq z} \mathbf{D}(z', z)$.

The temporal dynamics of host biomass h_i with evolving trait x_k, and of microbial biomass m_j with evolving trait y_s, can be described as:

$$\frac{d}{dt}h_i(t,x_k) = \underbrace{\sigma_{h_i}\sum_{k'=1}^{K}\mathbf{D}_h(x_k,x_{k'})\,h_i(t,x_{k'})}_{\textbf{diversification of host traits}}$$

$$+\,h_i\Big[\underbrace{f_{R_{h_i}}(x_k,\mathbf{H})}_{\textbf{host–host interactions}} + \underbrace{\sum_{j=1}^{J} f_{B_{h_i\leftarrow M_j}}(x_k,\mathbf{H},\mathbf{M}) - \sum_{j=1}^{J} f_{C_{h_i\rightarrow M_j}}(x_k,\mathbf{H},\mathbf{M})}_{\textbf{host–microbe interactions}}\Big],$$

$$\frac{d}{dt}m_j(t,y_s) = \underbrace{\sigma_{m_j}\sum_{s'=1}^{S}\mathbf{D}_m(y_s,y_{s'})\,m_j(t,y_{s'})}_{\textbf{diversification of microbial traits}}$$

$$+\,m_j\Big[\underbrace{f_{R_{m_j}}(y_s,\mathbf{M})}_{\textbf{microbe–microbe interactions}} + \underbrace{\sum_{i=1}^{I} f_{B_{m_j\leftarrow H_i}}(y_s,\mathbf{H},\mathbf{M}) - \sum_{i=1}^{I} f_{C_{m_j\rightarrow H_i}}(y_s,\mathbf{H},\mathbf{M})}_{\textbf{host–microbe interactions}}\Big].$$

where

$$\mathbf{H} = \big(h_i(x_k)\big)_{(i,k)\in I\times X} \quad \text{and } \mathbf{M} = \big(m_j(y_s)\big)_{(j,s)\in J\times Y}$$

An example of such an eco-evolutionary consumer-resource model is provided in the SI.

From consumer-resource feedbacks to multi-level selection

The multi-host and multi-microbe models discussed in the previous section can be extended to explicitly account for evolutionary processes (e.g., trait evolution), alongside ecological dynamics. The addition of the evolutionary components allows us to move beyond purely ecological predictions. It provides a mechanistic understanding of how resource-driven trait variation shapes partner associations, drives the evolution of interdependence, and determines the adaptive capacity of symbioses to change. By formalizing these eco-evolutionary feedbacks, such models link community interaction structure and resource dynamics to host and microbial evolution. Thus, these models effectively function as a multi-level selection framework.

Multi-level selection models have been useful in highlighting how the persistence of mutualistic host-microbe associations need not rely solely on high partner fidelity or strict parent to offspring transmission of symbionts. Instead, persistence can emerge from multi-level selection processes, including population- and community-level dynamics that favor beneficial host-microbe combinations (Roughgarden, 2020, 2023; Van Vliet and Doebeli, 2019; Bruijning et al., 2022; Lean and Jones, 2023; Gokhale et al., 2023). A limitation of current multi-level selection approaches, however, is their reliance on assumptions of timescale separation. These models are often implemented within adaptive dynamics frameworks and assume that microbial dynamics equilibrate before host reproduction. Consequently, their outcomes fail to capture how equilibria are shaped and created by ongoing feedbacks operating on comparable ecological and evolutionary timescales (Kopac and Klassen, 2016; Ashby et al., 2019; McGuinness et al., 2025; Song et al., 2015; Pichon et al., 2024; Malagon et al., 2025; Walmsley et al., 2025). Another key limitation is assuming, a priori, that selection occurs at particular fixed levels (e.g., microbial, host, or combined host-microbe or ‘holobiont’), which typically allows the strongest level to dominate and overlooks the emergence of new levels at which selection can act, or shifts in existing ones. As a result, these dynamics may fail to embody the compromises that can emerge among the sometimes competing interests across levels of selection.

Consider a case where within-host selection favours microbes with parasitic traits, but selection at the host level favours hosts associating with mutualistic microbes. Multi-level selection theory predicts that mutualistic traits can persist if selection at the group (or host) level outweighs selection within the microbial community. This persistence can be reinforced by limiting the recruitment or proliferation of parasitic microbes, through mechanisms such as host control or spatial structuring (Kiers et al., 2003; Brauchli et al., 1999; Sharp and Foster, 2022). Here we show that mutualist persistence may also arise from the coupling of ecological and evolutionary processes. In this case, persistence is an emergent eco-evolutionary property of the system rather than a consequence of host control, compartmentalization, or of other regulatory mechanisms. Because the ecological context both shapes and is shaped by trait evolution, eco-evolutionary feedbacks strongly influence community composition, and the balance of mutualists and parasites. The resulting community reflects the interplay of selective pressures, resource availability, and host-microbe interactions, as summarized in Fig. 2d. We refer to models capturing these feedback dynamics as 'eco-evolutionary consumer-resource models'.

To illustrate the consequences of relaxing timescale separation and quasi-static evolutionary assumptions, we simulate a minimal eco-evolutionary consumer-resource model of a host population interacting with a microbial community (Fig. 3). Microbes vary continuously in their investment in host resource provision, ranging from fully parasitic to fully mutualistic strategies. Additionally, microbes compete for a host-supplied resource that is shared indiscriminately among symbionts, conferring a competitive advantage to parasites. When ecological and evolutionary dynamics operate on different timescales, parasitic strategies dominate, driving a decline in mutualistic investment, host density, and ultimately community collapse (Fig. 3b(i)). In contrast, when ecological and evolutionary processes operate on comparable timescales, eco-evolutionary feedbacks generate a stable equilibrium characterized by the coexistence of parasitic and mutualistic symbionts and a positive host density (Fig. 3b(ii)). Unlike adaptive-dynamics frameworks, where evolution acts as a perturbation of an underlying ecological equilibrium (Dieckmann and Law, 1996; Geritz et al., 1998), here no meaningful ecological steady state exists independently of evolution. Rather stability emerges only when multi-level ecological interactions and evolutionary dynamics are considered simultaneously across scales.

Model analysis shows that ecological interactions between hosts and symbionts tend to increase host density in proportion to the average mutualistic investment of the symbiont community. In contrast, evolutionary dynamics (arising from a combination of selection and mutation) favor parasitic strategies, with this advantage increasing with resource abundance (Martignoni et al., 2024). As parasitism spreads, host density declines, weakening the advantage of parasitic symbionts and favoring a return toward mutualism. Thus, parasite abundance modulates host-associated resources and, in turn, the strength of selection for parasitic traits, altering the costs, benefits, and fitness associated with parasitism. The resulting feedback creates a new equilibrium with stable community composition and host abundance. Experimental observations of reduced virulence at low-density expansion fronts are consistent with these predictions (Raina et al., 2026; Nørgaard et al., 2021), highlighting the potential for the present framework to shed light on the eco-evolutionary processes leading to these patterns.

Notably, several existing approaches already examine how resource availability –whether externally supplied or produced internally by the population as shareable common goods– affects microbial community composition and trait evolution. These studies provide valuable guidance for defining expectations about resource-driven dynamics and for formulating resource- or density-dependent assumptions in modeling frameworks (Allen et al., 2016; Brown and Taddei, 2007; Ross-Gillespie et al., 2009; Sanchez and Gore, 2013; Kümmerli and Brown, 2010). Related bodies of work have also highlighted the non-intuitive consequences that arise when selection is contingent on changes in the resource landscape, including those generated by niche construction (Werner et al., 2025; Orr et al., 2025; Cheng et al., 2026; Jiang et al., 2023; Laland et al., 1999, 2016). These results indicate that neglecting the coupling between community structure, resource availability and selective pressure can significantly limit our ability to interpret host-microbe symbiosis dynamics, in which organisms simultaneously shape and respond dynamically to resources.

Eco-evolutionary consumer-resource models address this gap. Consideration of the interplay of ecological interactions, resource distribution, and selection allows the system's full behavior to emerge. As illustrated in Fig. 3, selective pressures on traits regulating resource supply arise from bottom-up-defined interaction functions, and drive context-dependent shifts from parasitism to mutualism. Trait diversification in parameters governing host or symbiont intrinsic growth (e.g., parameter r, see SI) may also help investigate the evolution of obligate symbiosis.

Our approach supports spatial extensions. Spatial dynamics can influence the availability of host- and microbe-associated resources by creating resource gradients or enhancing resource heterogeneity, thereby influencing community structure (Ledru et al., 2022; Martignoni et al., 2024; Cheng et al., 2026; Nørgaard et al., 2021). For example, mutualist-induced increases in local host density can amplify community-level competition, causing host declines in parasite-dominated regions and creating opportunities for more mutualistic host-symbiont associations to spread (Ledru et al., 2022). Spatially explicit models also provide a natural avenue for studying how dependency may affect the evolution of dispersal in symbiotic relationships (Narayanan and Shaw, 2024; Zilio et al., 2024; Cheng et al., 2026; Pichon et al., 2024). Finally, eco-evolutionary consumer-resource models can be extended to account for externally supplied resources and can incorporate additional layers of symbiotic interactions, such as mobile genetic element replicators within a host cell.

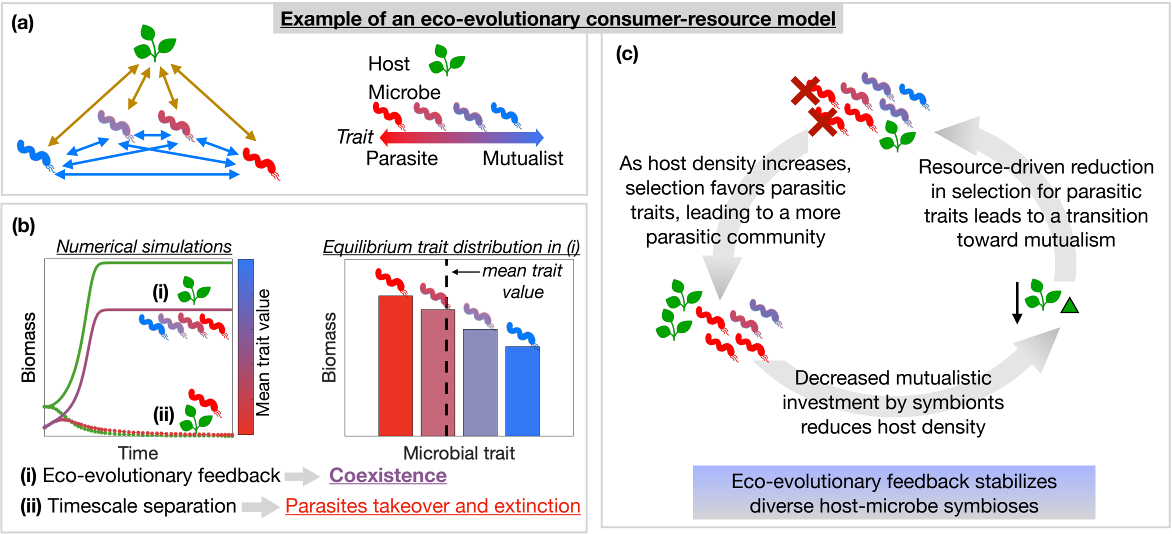


Fig. 3: Consumer-resource eco-evolutionary models generate emergent dynamics that are not accessible given standard timescale separation approaches. Coexistence dynamics of parasitic and mutualistic microbes emerge when feedback loops connecting consumer-resource dynamics to trait evolution, which here governs resource exchange, are fully considered. In the absence of coupling between ecological and evolutionary processes, the loop is interrupted, enabling parasite takeover and community collapse. By contrast, when processes operate on similar timescales, the feedback loop sustains coexistence of mutualists, parasites, and their host. (a) Model schematic, (b) numerical simulation outputs, and (c) qualitative eco-evolutionary feedback loop. See SI, and Martignoni et al. (2024) for full model formulation and parametrization.

Conclusion

Theoretical modeling of host-microbe symbioses is confronted with the need to bridge dynamics occurring at both micro- and macro-scales, while tracking the eco-evolutionary consequences of their interplay (Bordenstein, 2024; Ferretti et al., 2025). Thus, a reductionist approach is limited in its ability to characterize the population and evolutionary dynamics of symbiotic species. In host-microbe symbioses, community structure and evolution emerge from multi-scale interactions that modulate resource availability and thereby reconfigure selection and the levels at which selection acts.

We introduce an eco-evolutionary consumer-resource framework that provides a versatile tool that is flexible in its assumptions about degrees of integration and functional dependence, and moves beyond timescale separation to explore a broad spectrum of symbiotic outcomes. Such a framework can support the interpretation of experimental observations (Andrade-Domínguez et al., 2014; Sanchez and Gore, 2013; Schaffner et al., 2019; Zamorano et al., 2023; Rúa and Hoeksema, 2024; Nørgaard et al., 2021), and generate theoretical predictions about the persistence of symbioses under perturbation and change. Implications will span environmental health and therapeutics (Evensen et al., 2024; Ladau et al., 2025), as well as fundamental research on the emergence of biological organization (Kalambokidis and Travisano, 2024).

Acknowledgement

We thank Judith Bronstein, Austin Cruz, Adriana Dawes, and Christina Cobbold for insightful feedback and valuable comments on earlier versions of this manuscript.

Funding

This work was supported by the National Institutes of Health (NIH) (R01AI179743 and R01AI189624 to SRB); the Natural Sciences and Engineering Research Council of Canada (NSERC) (RGPIN-2022-03589 to RCT) and the UBC Okanagan Institute for Biodiversity, Resilience, and Ecosystem Services (to RCT); the National Science Foundation (NSF) (NSF-2321502 and NSF-2406985 to SPB); and the French National Research Agency (ANR) through project ReaCh (ANR-23-CE40-0023-01 to JG).

Supplementary information

Example of an eco-evolutionary consumer-resource model

To examine the effects of relaxing time-scale separation, we simulate a minimal eco-evolutionary consumer-resource model. Consider a host population with biomass density $H(t)$, interacting with a community of symbionts with total biomass density $M(t)$. Hosts provides a resource to their symbionts at a fix rate quantified by parameter β. Each symbiont provides another resource to the host at a rate quantified by parameter α. An example, is a plant host providing carbon to mycorrhizal fungi, and receiving phosphorus in exchange. We will call parameter α the 'mutualistic investment' of the symbionts.

The rate of mutualistic investment α is subject to diversification at rate d_m, i.e., α can evolve through genetic or phenotypic variation over time. Thus, the microbial community includes symbionts that differ in their mutualistic investment, such that the total symbiont biomass M at time t is given by integrating the symbiont biomass density $m(t, \alpha)$ over the trait space α:

$$M(t) = \int_{\alpha_{\min}}^{\alpha_{\max}} m(t,\alpha)\, d\alpha\,. \tag{1}$$

The maximal mutualistic investment of a symbiont is given by parameter $\alpha_{\max} > 0$. Here, we consider $\alpha_{\min} = 0$, meaning that in this case the symbiont does not provide anything to the host. Note that more parasitic symbionts receive the same amount of resource from the host as more mutualistic symbionts, but at a lower (or zero) cost, and have therefore a selective advantage. The net benefit to the host population depends on the average mutualistic investment $\bar{\alpha}(t)$ of the symbiont population as a whole. At time t, $\bar{\alpha}$ is given by

$$\bar{\alpha}(t) = \int_{0}^{\alpha_{\max}} \alpha\, \frac{m(t,\alpha)}{M(t)}\, d\alpha \tag{2}$$

We thus obtain the following eco-evolutionary consumer-resource model:

$$\partial_t H = H\Big[\underbrace{(r - \mu_h H)}_{f_R(H)} + \underbrace{Q\,\bar{\alpha}(t)\,\frac{M}{H+d}}_{f_{B_{H\leftarrow M}}} - \underbrace{\beta M}_{f_{C_{H\to M}}}\Big], \tag{3a}$$

$$\partial_t m(t,\alpha) = \underbrace{d_m \partial_\alpha^2 m}_{\substack{\text{trait}\\ \text{diversification}}} + m\Big[- \underbrace{\mu_m M}_{f_{R_m(\alpha,M)}} + \underbrace{\beta H}_{f_{B_{m(\alpha)\to H}}} - \underbrace{\alpha\,\frac{H}{H+d}}_{f_{C_{m(\alpha)\leftarrow H}}}\Big], \quad \alpha \in (0, \alpha_{\max})\,. \tag{3b}$$

No-flux boundary conditions are imposed at the lower and upper limits of the trait domain $(0, \alpha_{\max})$, such that

$$\partial_\alpha m(t,0) = \partial_\alpha m(t,\alpha_{\max}) = 0, \quad \text{for all } t > 0.$$

Note that H, M, and m have been converted into dimensionless quantities with arbitrary units.

Interaction functions

- *Host and microbe-microbe interactions*: The host follows logistic growth, as described by the function f_{R_H}. Microbes are obligate mutualists, and their density is regulated by competition, both within and between strains with different traits, as described by the function $f_{R_m}(\alpha, M)$. This term captures microbe-microbe competition for shared host resources, where strain characterized by low (or zero) mutualistic investment present a competitive advantage.

- *Host-microbe interactions*: Resource provision from the host to the symbionts depends linearly on host and symbiont densities (see functions $f_{C_{H\to M}}$ and $f_{B_{m(\alpha)\leftarrow H}}$). Resource provision from the symbionts to the host increases linearly with increasing symbiont density, and nearly linearly with increasing host density when host density is low (relative to parameter d) (see functions $f_{C_{m(\alpha)\to H}}$ and $f_{B_{H\leftarrow m(\alpha)}}$). When host density is large (relative to d) resource provision tends toward a dependency on symbiont density only, as we assume host availability to not be a factor limiting the resource provision capacity of symbionts. The efficiency of the conversion of resources into host and symbiont biomass is determined by parameter Q (see Martignoni et al. (2020b)). These functions are deliberately minimal to allow analytical progress, while remaining mechanistically grounded and biologically interpretable.

Within this framework, mathematical tools –such as spectral analysis and equilibrium analysis of ordinary differential equations– yield both qualitative and quantitative insights into model equilibria. In particular, they allow us to characterize the mean mutualist investment of the symbiont population, and the full equilibrium distribution of traits. In addition, tools from ancestral process theory provide insight into the dynamics of ancestral lineages within the symbiont population. This approach allows us to identify the most likely common ancestor at equilibrium, and to quantify the fixation probability of each trait. Notably, for this model we find that the most likely common ancestor of a mutualist is a parasitic symbiont (Martignoni et al., 2024). The code used to produce Fig. 3 is publicly available on Zenodo (https://doi.org/10.5281/zenodo.18396556).

Eco-evolutionary feedback: In Fig. 3b, we compare the outcomes of the model described above for a situation in which: (i) Trait evolution and ecological interactions occur at comparable timescales (i.e., $d_m > 0$); and (ii) trait evolution and ecological interactions occur at separate timescale. This distinction can be done by considering that the rate of trait diversification $d_m = 0$, indicating that ecological competition is fast with respect to evolutionary changes.

When ecological interactions are considered in isolation, symbionts with parasitic traits will take over in the community, due to their competitive advantage. As a consequence, the mean mutualistic investment of the population will decrease, and host density with it, leading to the collapse of the whole community (Fig. 3b(ii)). However, when ecological and evolutionary processes occur at comparable timescales (i.e., as soon as $d_m > 0$), the symbiont population reaches an equilibrium distribution, as shown in Fig. 3b(i), and host density remains positive. Importantly, an equilibrium distribution is reached for any positive value of d_m, with the equilibrium depending on all model parameters and derivable analytically.

Analysis of the model (performed in Martignoni et al. (2024)) shows that ecological interactions between hosts and symbionts increase host density in proportion to the average mutualistic investment of the symbiont community. Indeed, at equilibrium, ecological interactions between host and symbiont result in the following host density

$$h = d\left(\frac{\bar{\alpha}}{\alpha_c} - 1\right), \quad \text{with} \quad \alpha_c = \frac{\beta\, d}{Q}\,\frac{(Q+1) - \sqrt{(Q-1)^2 - 4\dfrac{Q\mu_m\mu_p}{\beta^2}}}{2}\,. \tag{4}$$

In contrast, evolutionary dynamics (as a combination of selection and mutation) favor more parasitic symbionts, which gain a fitness advantage that increases with resource availability and, consequently, with host density. Specifically, the resulting balance between selection and mutation produces a trait distribution as a function of host density h that can be approximated by the Airy function truncated at $\alpha_{\max}$, with mean $\bar{\alpha}$ satisfying

$$\bar{\alpha} = z_0\left(\frac{(p+d)d_m}{p}\right)^{1/3}, \tag{5}$$

where z_0 is a positive constant that depends only on the Airy function solving the dimensionless problem $\mathrm{Ai}''(z) - z\,\mathrm{Ai}(z) = 0$ on $\mathbb{R}$.

Thus as parasitic strategies become more prevalent, the average mutualistic investment declines, leading to reduced host density and weakening the fitness advantage of parasitism. This shift promotes a return toward more mutualistic strategies, which again raise host density and restore the advantage of parasitic symbionts. The opposing forces of microbe-level selection for parasitism and higher-level selection for mutualism thus stabilize host density around a fixed value.

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