An eco-evolutionary consumer-resource theory of host-microbe symbioses

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Abstract

Symbiotic associations between microorganisms and hosts are universal, diverse, and dynamic. Yet, our ability to represent this complexity mathematically remains limited. We propose extending consumer–resource theory to incorporate evolutionary processes to advance our understanding of symbioses, from pairwise interactions to complex host–microbe assemblages. The resulting eco-evolutionary framework captures feedbacks between host–microbe interaction structure, biotic resource availability, and selection acting across biological scales. Importantly, this approach relaxes the assumption of separated ecological and evolutionary timescales, so that both processes unfold simultaneously. The coupling between ecological and evolutionary dynamics allows key properties of symbioses, such as ecological dependence and functional integration, to emerge from evolving resource-mediated interactions, rather than being imposed a priori. We illustrate the framework with a mathematical model of mycorrhizal symbiosis. The proposed consumer–resource formulation provides a unified basis for linking ecological and evolutionary dynamics in host–microbe symbioses, with implications for both basic theory and applied management.

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

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Introduction

Toward a theory of living together

Host-microbe symbioses are essential components of the biosphere, with profound ecological and economic significance. Canonical interactions involve eukaryotic hosts that associate with a multitude of microbial species. Examples of these associations 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 incomplete and overly simplified (Araujo et al., 2024; Ferretti et al., 2025; Week et al., 2025b).

The evolutionary and population dynamics of host-microbe symbioses can differ fundamentally from those of their component single species, due to emergent properties of multi-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 (Paracer and Ahmadjian, 2000). Together, these interacting processes create reciprocal ecological and evolutionary feedbacks, whereby changes in one partner alter the selective environment experienced by the other (Douglas, 2015; Brooks et al., 2016). Consequently, the ecological and evolutionary dynamics of hosts and their symbionts cannot always be understood in isolation (Fig. 1). This holistic perspective spurred the development of holobiont biology, emphasizing that biological form and function can emerge from the composition of symbiotic communities and the associations among their members (Bordenstein, 2024).

Theoretical advancements offer a path to clarify how host-microbe interactions and their interdependence shape symbiosis dynamics and evolution (Ferretti et al., 2025; Araujo et al., 2024; Week et al., 2025b). Pioneering work in symbiosis modeling has begun to untangle the eco-evolutionary pathways underlying a fuller spectrum of symbiotic dynamics (Araujo et al., 2026; Week et al., 2025a; Pearman et al., 2025; Roughgarden, 2023; de Azevedo-Lopes and Traulsen, 2026; Bruijning et al., 2022). This work spans a range of complementary approaches, including evolutionary game theory (Akçay, 2015; Gokhale et al., 2023), quantitative genetics (Week et al., 2025a; Fisher et al., 2017), multilevel selection models (Roughgarden, 2023; Pearman et al., 2025; de Azevedo-Lopes and Traulsen, 2026), phenomenological ecological models (Araujo et al., 2026; Faust and Raes, 2012), and metabolic network frameworks (Jyoti et al., 2026; Dicenzo et al., 2020), each emphasizing different aspects of how symbiotic associations form, function, persist, evolve, and respond to environmental change. For instance, evolutionary game theory and population genetics emphasize trait evolution and fitness consequences, often under simplified ecological structure (Axelrod and Hamilton, 1981; Foster and Wenseleers, 2006). Similarly, multilevel selection and neutral assembly models have been developed to formalize how selection operates on collective microbiome configurations across generations (Price, 1972; Damuth and Heisler, 1988; Zilber-Rosenberg and Rosenberg, 2008). In contrast, ecological models –such as generalized Lotka–Volterra equations– capture population dynamics and community assembly but typically treat traits as static parameters (Faust and Raes, 2012; Stein et al., 2013). Metabolic network models, on the other hand, resolve fine-scale resource exchange but are difficult to scale to eco-evolutionary dynamics at the community level (Manor et al., 2014; Succurro and Ebenhöh, 2018). Together, these approaches have revealed important principles governing symbiotic interactions, yet a mechanistic framework that simultaneously links evolving traits, population dynamics, and resource dynamics

remains lacking.

Here, we propose consumer–resource theory as a complementary and mechanistic perspective that has so far been underutilized in symbiosis modelling. Rooted in foundational ecological theory, the consumer-resource framework links population dynamics to limiting environmental resources, such as nutrients or energy fluxes (Tilman, 1982; Chase and Leibold, 2009). When applied to symbioses –literally 'living together'– a consumer–resource perspective reframes interacting partners as components of each other's biotic environment, where resource availability is dynamically shaped by their interactions (Holland and DeAngelis, 2010). Building on this ecological foundation, we propose extending consumer–resource theory to incorporate evolutionary dynamics within the same mechanistic framework. This approach allows ecological and evolutionary processes to be considered jointly through resource-mediated interactions.

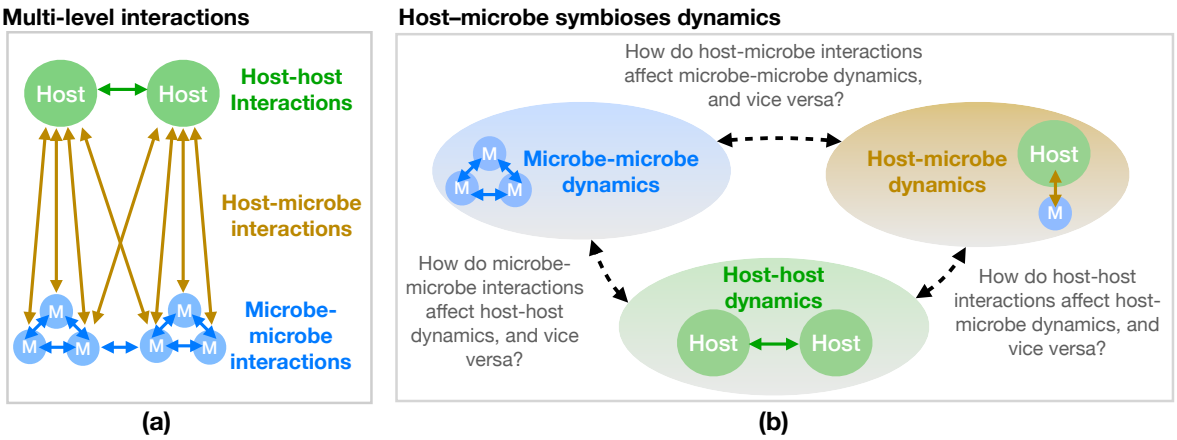

Fig. 1: Host-microbe symbioses are multi-level, dynamical systems. (a) A schematic representation of multi-level population structure and dynamics characteristic of host-microbe symbioses. (b) Interactions among hosts, between hosts and microbes, and among microbes can influence one another, collectively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

Symbioses as reciprocal consumer–resource dynamics

The consumer–resource eco-evolutionary formulation we develop sits on a simple conceptual framing: the host's resource environment is modulated (positively and negatively) by its microbial symbionts, and concurrently the microbial resource environment is shaped by the 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 (Feng et al., 2019; Salem et al., 2014). In this way, interactions among hosts and microbes influence not only community structure, but also the availability of biotic resources for hosts and symbionts. This framing suggests that host-microbe symbioses can be naturally modeled as reciprocal consumer-resource dynamics.

Originally developed to describe competition for shared resources (Fig. 2a) (Tilman, 1982; Chase and Leibold, 2009), consumer–resource models have more recently been extended to describe a broader range of interaction types, including mutualism (Fig. 2b) (Holland and DeAngelis, 2010). Consumer-resource models of mutualism provide a mechanistic basis for linking resource acquisition and exchange to the resulting biomass dynamics of interacting species. In this formulation, resources supplied, consumed, or converted by interacting partners mediate their interactions, with resource exchange shaped by underlying species traits. Despite their name, these models are not limited to mutually beneficial associations. Differences in the net costs and benefits of exchange determine interaction outcomes, allowing

this class of consumer–resource models to represent a continuum from mutually beneficial to mutually harmful interactions. The functional forms describing resource exchange –including both benefits and costs– can be linear, saturating, or empirically grounded in more complex relationships (Holland et al., 2002; Holland and DeAngelis, 2010). These relationships can incorporate density dependence, such that resource availability and biomass conversion depend on species densities (e.g. Bachelot and Lee (2018); Martignoni et al. (2020b)). This formalism is therefore well suited to describing host–microbe symbioses, where interacting partners are coupled through resource exchange.

To date, consumer-resource models of mutualism have primarily focused on two-species systems, examining the conditions for ecological stability of mutually beneficial relationships, including mutualistic symbioses (Hale and Valdovinos, 2021; Holland, 2015; Osuna et al., 2025). Recent extensions have successfully expanded these models to multi-species communities (Fig. 2c), revealing mechanisms that maintain microbial diversity and coexistence in symbiotic communities (Bachelot and Lee, 2018; Valdovinos, 2019; Martignoni et al., 2020b,a). However, these frameworks almost universally assume fixed traits and static interaction structures. As a result, they can characterize the ecological consequences of established relationships, but cannot account for evolutionary transitions along the parasitism-mutualism continuum or for the emergence of mutualism itself.

In host-microbe symbioses, selection pressures arise from ecological context –such as host density, microbial density, interspecific competition, and resource depletion– which are themselves shaped by host and symbiont traits (Douglas, 2015; Brooks et al., 2016). Capturing these reciprocal feedbacks requires explicitly integrating evolutionary dynamics, enabling symbiont and host traits to respond to and reshape the ecological conditions that generate selection. Community structure then emerges from the interplay between selective pressures, resource availability, and host–microbe interactions (Fig. 2d). In the next section, we walk through a concrete example to show how trait evolution and resource exchange can be integrated within a consumer–resource framework.

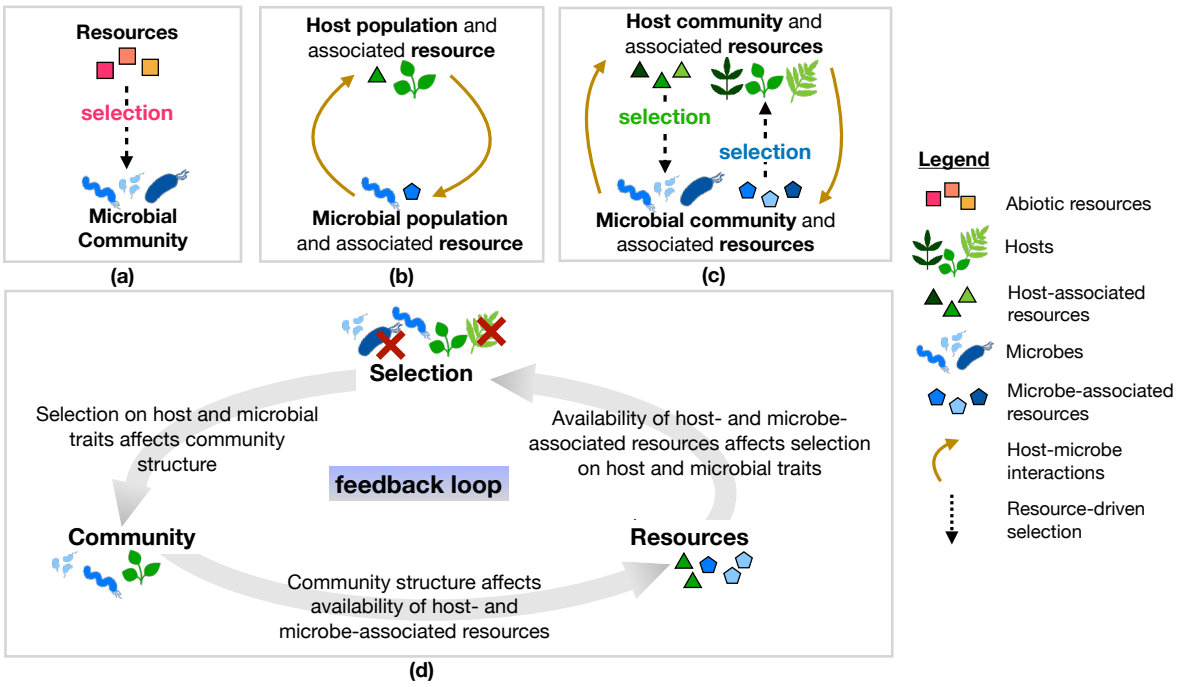

Fig. 2: Reciprocal resource exchange links partner traits to community dynamics and selection. (a) Resource availability influences ecological dynamics through the structure of consumer–resource interactions. (b) Consumer–resource interactions in which two parties (e.g., host and symbiont) simultaneously act as both consumers and resource providers. (c) The interacting parties in (b) are replaced by whole communities (e.g., microbial and host populations). Resource-mediated interactions between communities shape population dynamics and community composition, with ecological interactions generating selection on existing trait variation. (d) Extending the community framework in (c) to incorporate trait evolution generates eco-evolutionary feedbacks. Selection shapes host and microbial trait composition, trait composition modifies resource exchange and community dynamics, and the resulting changes in resource availability in turn modify selection.

An eco-evolutionary consumer–resource model

We present a minimal model to illustrate how evolutionary dynamics can be coupled to ecological interactions in consumer–resource frameworks, based on the work of Martignoni et al. (2024). Consider a host population with biomass density $H(t)$, interacting with a community of symbionts with total biomass density $M(t)$ (Fig. 3a). Hosts provide a resource to their symbionts at a fixed rate quantified by parameter β. In return, symbionts provide resources to the host at a rate determined by trait value α, which we refer to as the mutualistic investment of the symbiont. As a concrete example, plant hosts may provide carbon to mycorrhizal fungi while receiving phosphorus in return. Symbionts compete equally for the resource supplied by the host, which is shared indiscriminately among symbionts, with the strength of competition governed by parameter μ_m. Because resource allocation is independent of trait value, symbionts with lower mutualistic investment α receive the same resources while incurring lower costs, thereby gaining a competitive advantage over more mutualistic strains.

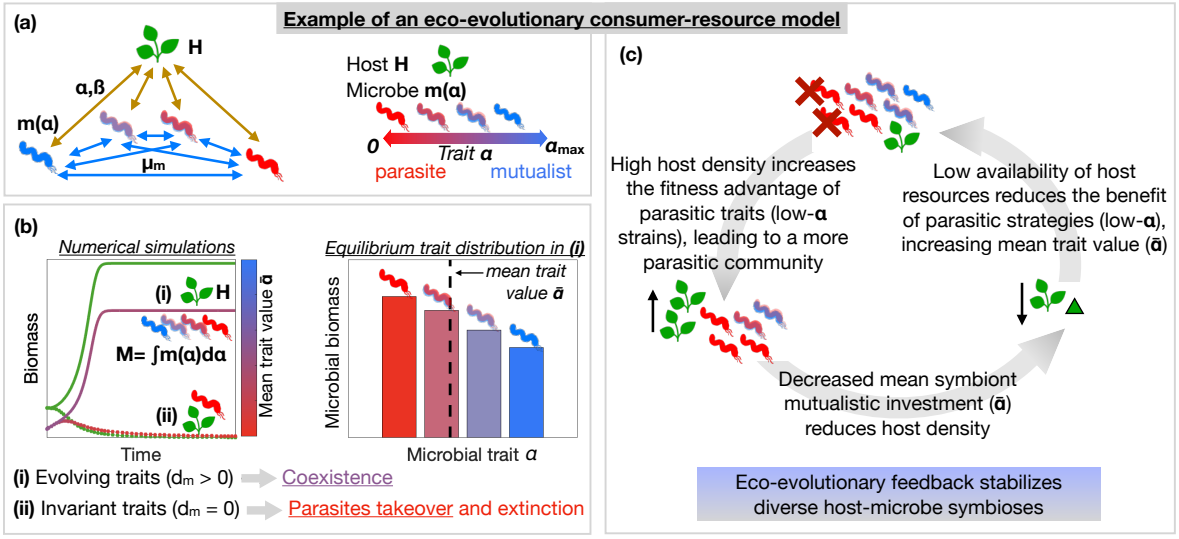

Fig. 3: Eco-evolutionary consumer–resource feedbacks maintain coexistence between mutualists and parasites. Coexistence emerges when consumer–resource dynamics and trait evolution, mediated by resource exchange, are explicitly coupled. In the absence of trait variation ($d_m = 0$), selection drives the community toward parasitism, leading to reduced host density and eventual collapse. By contrast, when evolutionary change is enabled ($d_m > 0$), trait variation allows different strategies to respond to resource-mediated selection, generating feedbacks between trait composition and resource dynamics that stabilize coexistence between mutualists, parasites, and their host. (a) Model schematic (see Eq. (3)). Brown arrows denote resource exchange through host–microbe interactions (characterized by parameters α and β), while blue arrows denote resource competition among microbes (parameter μ_m). (b) Numerical simulation outputs. (c) Schematic representation of the eco-evolutionary feedback generating coexistence.

Trait diversification

To capture evolutionary changes in mutualistic investment, we allow trait α to diversify in trait space. Here, this process is modeled as Gaussian diffusion with diffusion coefficient d_m. Growth of biomass within a trait class represents the persistence and propagation of existing trait values, while diffusion represents heritable variation through asexual reproduction, with offspring traits distributed around parental values according to a Gaussian distribution with fixed variance. As the microbial community consists of symbionts spanning a range of mutualistic investment values, the total microbial biomass $M(t)$ at time t is obtained by integrating the biomass density $m(t, \alpha)$ over trait space:

$$M(t) = \int_0^{\alpha_{\max}} m(t, \alpha)\, d\alpha\,. \tag{1}$$

The maximal mutualistic investment is given by $\alpha_{\max} > 0$, while $\alpha = 0$ corresponds to symbionts that provide no resources to the host. Thus, symbionts vary continuously in their investment in host resource provision, ranging from fully parasitic ($\alpha = 0$) to maximally mutualistic ($\alpha = \alpha_{\max}$). 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 formulate the following eco-evolutionary consumer–resource model:

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

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

Here, functions R, B, and C describe intrinsic population growth and within-population regulation, interaction-derived benefits, and interaction-derived costs, respectively. 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. The biological interpretations and specific functional forms of R, B, and C are provided in detail below.

Ecological interactions

- **Host and microbe-microbe interactions**: The host follows logistic growth, with growth function

$$R_H = r - \mu_h H\,. \tag{4}$$

  Here, microbes are modeled as obligate symbionts (such as arbuscular mycorrhizal fungi), and are incapable of growth in the absence of the host. Microbial growth is regulated by density-dependent competition, both within and between strains with different trait values, according to

$$R_m(\alpha) = -\mu_m M = -\mu_m \int_0^{\alpha_{\max}} m(t,\alpha)\,d\alpha. \tag{5}$$

  This term captures competition among symbionts for host-derived resources. Strains investing less in mutualism (low α) incur lower costs, allowing them to attain higher biomass and thereby gain a competitive advantage.

- **Host-microbe interactions**: Resource provision from the host to the symbionts ($H\to M$) depends linearly on host and symbiont densities. We assume that the host's resource investment is entirely transferred to the symbiont community, with all symbiont biomass receiving the same resource input regardless of trait value. The corresponding rates of cost (to the host) and benefit (to the symbionts) arising from resource exchange are given by

$$C_{H\to M} = \beta M \quad \& \quad B_{m(\alpha)\leftarrow H} = \beta H\,. \tag{6}$$

  Resource provision from the symbionts to the host ($m(\alpha)\to H$) depends on host availability and the symbiont trait value α. We assume that symbionts with trait value α contribute to host growth at a rate that increases with host density but eventually saturates. The saturating functional form reflects the finite capacity of symbionts to export resources, causing per-capita symbiont contributions to plateau at high host densities. The resulting rates of cost (to the symbionts) and benefit (to the host) are given by

$$B_{H\leftarrow m(\alpha)} = Q\,\bar{\alpha}(t)\,\frac{M}{H+d} \qquad \& \qquad C_{m(\alpha)\to H} = \alpha\,\frac{H}{H+d}. \tag{7}$$

In the limit of large host density relative to d, the total benefit to the host is proportional to symbiont density and the community mean trait value $\bar{\alpha}$. The dimensionless parameter Q represents the relative efficiency of converting exchanged resources into host and symbiont biomass (see Martignoni et al. (2020b)). These functions are deliberately minimal to allow analytical progress, while remaining mechanistically grounded, biologically interpretable, and amenable to experimental parameterization (Martignoni et al., 2021).

Eco-evolutionary feedback

We compare the outcomes of the model under two scenarios: (i) ecological and evolutionary processes occur on comparable timescales ($d_m > 0$); and (ii) the limiting case in which evolutionary change is absent ($d_m = 0$), such that ecological dynamics unfold without trait diversification (Fig. 3b). When traits are effectively invariant ($d_m = 0$), ecological interactions alone lead to the dominance of parasitic symbionts due to their competitive advantage. As a consequence, the mean mutualistic investment of the symbiont population ($\bar{\alpha}$) decreases, leading to a decline in host density and eventually to community collapse, depending on the host's intrinsic growth rate (Fig. 3b(ii)). In contrast, when evolutionary and ecological processes act on comparable timescales ($d_m > 0$), trait variation allows the symbiont population, including both mutualists and parasites, to reach a stationary trait distribution, ensuring a positive host density at equilibrium (Fig. 3b(i)). Importantly, any positive value of d_m, however small, is sufficient to maintain a positive host density at equilibrium and prevent community collapse (Martignoni et al., 2024).

The described outcomes can be understood more formally using spectral and equilibrium analysis (Alfaro et al., 2021), allowing characterization of the mean mutualistic investment of the symbiont community alongside the full equilibrium distribution of traits. Model analysis (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. At ecological equilibrium, host density is given by

$$H = d\left(\frac{\bar{\alpha}}{\alpha_c} - 1\right), \quad \text{with} \quad \alpha_c = \frac{\beta\, d}{Q}\,\frac{(Q+1) - \sqrt{(Q-1)^2 - 4\dfrac{Q\mu_m\mu_h}{\beta^2}}}{2}, \tag{8}$$

where α_c denotes a critical threshold in mean mutualistic investment separating regimes of host persistence and collapse. In parallel, evolutionary dynamics favor parasitic strategies, with this advantage increasing with resource abundance. Indeed the resulting balance between selection and trait diversification produces a trait distribution that depends on host density H, which can be approximated by an Airy function truncated at $\alpha_{\max}$, with mean satisfying

$$\bar{\alpha} = z_0\, d_m^{1/3}\left(1 + \frac{d}{H}\right)^{1/3} \tag{9}$$

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 $\mathbb{R}$.

Together, Eqs. (8) and (9) reveal a stabilizing eco-evolutionary feedback. Ecologically, equilibrium host density increases with the mean mutualistic investment $\bar{\alpha}$ (Eq. (8)). Evolutionarily, however, the equilibrium mean investment depends inversely on host density through the term d/H (Eq. (9)): As host density decreases, d/H increases, shifting the trait distribution toward higher mean mutualistic investment. Thus, a decline in host density reduces the ecological benefit of parasitic strategies and favors higher mutualistic investment, which

in turn promotes host persistence. Conversely, higher host density reduces d/H, favoring lower mutualistic investment and thereby weakening the positive feedback on the host. The interplay between these opposing ecological and evolutionary forces, combined with ongoing generation of trait variation, stabilize host density around an equilibrium value, while allowing coexistence of parasitic and mutualistic symbionts (Fig. 3c).

Notably, ancestral process theory (Forien et al., 2022) shows that the most likely common ancestor of a mutualistic symbiont is, counterintuitively, a parasitic one (Martignoni et al., 2024). This result emerges because high abundance of parasitic lineages provides a larger pool from which mutualistic strategies can arise through trait diversification. This example illustrates how eco-evolutionary consumer–resource models can reveal non-intuitive mechanisms governing the stability and persistence of symbioses. A generalized formulation of the eco-evolutionary consumer–resource framework is presented in Box 1, providing a flexible foundation for application to diverse host–microbe systems and broader eco-evolutionary contexts.

A mechanistic foundation for symbiotic evolution

From consumer–resource feedbacks to emergent evolutionary organization

A central challenge for theoretical models of symbioses is understanding how selection acting at different organizational levels shapes evolutionary outcomes, from interactions within host-associated microbial communities to selection among host individuals (de Azevedo-Lopes and Traulsen, 2026; Lean and Jones, 2023; Week et al., 2025b). Multi-level selection theory provides a framework for partitioning evolutionary change into contributions from selection acting within and between groups, where groups can represent different biological levels of organization, such as individual microbes and hosts, host–microbe assemblages (or holobionts), or broader communities (Lewontin, 1970; Price, 1972; Okasha, 2006). In host–microbe symbioses, this perspective has been particularly useful for understanding how cooperative associations can persist despite opposing selective pressures within microbial communities and among hosts (Zeng et al., 2017; Bruijning et al., 2022; Van Vliet and Doebeli, 2019; Roughgarden, 2023, 2020; Pearman et al., 2025). Such persistence is often explained by mechanisms that align fitness across levels, including partner fidelity (Frederickson, 2013), host control (Sharp and Foster, 2022), or spatial structuring (Brauchli et al., 1999) that limit the spread of selfish strategies. More recent developments in multi-level selection theory have also emphasized that ecological interactions and population structure can generate the conditions under which selection among levels becomes relevant, rather than treating levels of selection as independent of ecological processes (Doulcier et al., 2020; Luo, 2014; Van Vliet and Doebeli, 2019).

The consumer–resource perspective developed here complements these approaches by explicitly representing the ecological mechanisms that generate the selective environments in which multi-level dynamics emerge. Within this framework, higher-level properties such as host density and community composition are not imposed a priori as predefined units of selection or hierarchical levels at which fitness is evaluated. Instead, they emerge from feedbacks between trait evolution and ecological interactions: Changes in symbiont traits alter resource exchange, which reshapes population- and community-level dynamics and feeds back on selection. This formulation provides a bottom-up route to understanding how higher-level organization and selective dynamics arise from coupled ecological and evolutionary processes.

Expanding the scope of consumer-resource models

The framework developed here provides a general representation of how trait evolution can be coupled to consumer–resource dynamics in symbiotic systems. The example of Fig. 3

illustrates one application, in which evolution acts on traits governing resource exchange, represented by the benefit and cost functions B and C (Eqs. (6) and (7)). The generalized formulation presented in Box 1 extends this approach by allowing evolutionary change to act on a broader class of traits, including those governing host and microbial intrinsic growth, represented by the functions R_h and R_m. Allowing these growth functions to evolve, for example, provides a basis for studying how interdependence itself may evolve through eco-evolutionary feedbacks.

Host and microbial traits could also evolve simultaneously, such that both microbial and host biomass densities $m(y_s)$ and $h(x_k)$ become structured by their respective traits (see Box 1). Such models would provide a setting for studying interspecific epistasis, where the fitness consequences of a trait in one partner depend on the traits expressed by the other, and for exploring how selection acts on interacting trait combinations during coevolution. More broadly, consumer–resource eco-evolutionary models can be expanded to incorporate additional components of symbiotic dynamics, including externally supplied resources, multiple interacting microbial partners, and mobile genetic elements within host-associated communities.

A complementary extension is to incorporate spatial structure, which can modify the ecological context in which resource-mediated interactions and evolutionary dynamics unfold. Spatial dynamics can influence the distribution and availability of host- and microbe-associated resources by creating resource gradients or enhancing resource heterogeneity, thereby shaping community structure and evolutionary trajectories (Ledru et al., 2022; Martignoni et al., 2024; Cheng et al., 2026). For example, mutualist-induced increases in local host density can amplify community-level competition, disadvantaging hosts in regions dominated by parasitic symbionts and creating opportunities for more mutualistic host–symbiont associations to spread (Ledru et al., 2022). Spatially explicit extensions also provide an avenue for studying how dependence between partners influences the evolution of dispersal and spatial dynamics in symbiotic systems (Narayanan and Shaw, 2024; Zilio et al., 2024; Nørgaard et al., 2021).

Box 1: Eco-evolutionary consumer-resource models

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

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

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 R_{h_i} and 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 interactions**, through benefit functions $B_{h_i \leftarrow M_j}$ and $B_{m_j \leftarrow H_i}$, and cost functions $C_{h_i \rightarrow M_j}$ and $C_{m_j \rightarrow H}$. 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:

$$\frac{d}{dt} h_i(t, x_k) = \underbrace{\sigma_{h_i} \sum_{k'=1}^{K} \mathbf{D}_h(x_k, x_{k'})\, h_i(t, x_{k'})}_{\substack{\text{diversification of} \\ \text{host traits}}} + h_i \Big[\underbrace{R_{h_i}(x_k, \mathbf{H})}_{\substack{\text{host–host} \\ \text{interactions}}} + \underbrace{\sum_{j=1}^{J} B_{h_i \leftarrow M_j}(x_k, \mathbf{H}, \mathbf{M}) - \sum_{j=1}^{J} C_{h_i \to M_j}(x_k, \mathbf{H}, \mathbf{M})}_{\text{host–microbe interactions}} \Big],$$

$$\frac{d}{dt} m_j(t, y_s) = \underbrace{\sigma_{m_j} \sum_{s'=1}^{S} \mathbf{D}_m(y_s, y_{s'})\, m_j(t, y_{s'})}_{\substack{\text{diversification of} \\ \text{microbial traits}}} + m_j \Big[\underbrace{R_{m_j}(y_s, \mathbf{M})}_{\substack{\text{microbe–microbe} \\ \text{interactions}}} + \underbrace{\sum_{i=1}^{I} B_{m_j \leftarrow H_i}(y_s, \mathbf{H}, \mathbf{M}) - \sum_{i=1}^{I} C_{m_j \to H_i}(y_s, \mathbf{H}, \mathbf{M})}_{\text{host–microbe interactions}} \Big].$$

where

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

A continuous representation of symbioses: Host–microbe resource exchange is determined by the balance between benefit and cost terms B and C, and can vary continuously in both sign and magnitude. Growth functions R determine the degree of ecological dependence, ranging from facultative to obligate interactions depending on the extent to which hosts and microbes can sustain growth in the absence of their symbiotic partners. Thus, variation in B, C, and R provides a continuous representation of interaction type, interaction strength, and ecological dependence. Evolution acting on the traits underlying these functions enables temporal changes in intrinsic growth and resource exchange, allowing degrees of functional integration and dependence to emerge through eco-evolutionary feedbacks.

Connections and integration across eco-evolutionary theory

A central feature of eco-evolutionary consumer-resource frameworks is that resources are not treated solely as external constraints, but as dynamic components of ecological interactions shaped by organisms themselves. This view connects consumer-resource approaches to sym-

biosis with broader developments in ecological and evolutionary theory, including niche construction and theories of environmental modification, which emphasize how organisms reshape the environments that subsequently influence their evolution (Laland et al., 1999, 2016; Gefen et al., 2026). Similarly, research on microbial cooperation and public goods has shown how organisms can modify shared resource landscapes, generating feedbacks between resource availability, community composition, and the evolution of cooperative traits (Ross-Gillespie et al., 2009; Sanchez and Gore, 2013; Kümmerli and Brown, 2010). In symbiotic systems, these ideas take on a reciprocal form, as partners simultaneously modify and respond to one another's ecological environments. Bringing together consumer–resource approaches to symbiosis with theories of environmental modification, niche construction, and cooperation may reveal common principles underlying how organisms reshape the selective environments to which they respond.

The mechanistic advantage of consumer-resource models makes them particularly suited for studying metabolite-mediated interactions, including nutrient exchange and cross-feeding dynamics (Goldford et al., 2018; Marsland III et al., 2019). However, the same mechanistic focus also defines the processes that are better represented within this framework. Many host–microbe interactions involve additional interaction modes –including contact-dependent antagonism, immune modulation, and signalling (Hooper et al., 2012; Nyholm and McFall-Ngai, 2021; Russell et al., 2014)– that are not readily captured in a resource-centered formulation. Similarly, processes such as stochastic community assembly, transmission between hosts, and metacommunity dynamics are often better represented in alternative frameworks, including individual- or agent-based models (Hellweger et al., 2016; Zeng and Rodrigo, 2018), mutualistic network models (Cai et al., 2020; Guimaraes Jr, 2020), and metacommunity approaches (Sarkar et al., 2026; Miller and Bohannan, 2019). Finally, while a mechanistic approach can be well suited for systems with continuous spatial structure, such as the rhizosphere, systems with discrete spatial structure, such as animal hosts, may also be more naturally represented using individual-based or agent-based multilevel selection models (Roughgarden, 2023; Doulcier et al., 2020).

These complementary strengths suggest the need for a more explicit integration of theoretical perspectives on symbiosis. A key challenge for future work is to clarify how mechanistic trait-based descriptions, fitness-based abstractions, and population-level formulations relate to one another, and to make explicit the assumptions underlying each approach. Such integration would help bridge bottom-up ecological mechanisms with descriptions of higher-level organization, situating different models within a broader eco-evolutionary understanding of symbioses rather than treating them as isolated modelling traditions.

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). Reductionist approaches can therefore struggle to capture how community structure, resource exchange, and evolutionary dynamics jointly shape the persistence and transformation of symbiotic associations. In host–microbe symbioses, community structure and evolution emerge from multi-scale interactions that modulate resource availability and thereby reshape selective pressures and the ecological contexts in which they operate.

Consumer–resource theory provides a mathematical language in which ecological organization emerges from patterns of resource exchange without requiring predefined biological entities or levels of selection. In this view, resource fluxes, biomass dynamics, and ecological interactions are regarded as fundamental quantities, while variable properties often discussed

in the context of holobiont biology –such as ecological dependence and functional integration– can emerge from the structure and dynamics of these interactions. Developing such resource-centered descriptions may help connect traditionally separate approaches to symbiosis and, more generally, contribute toward a unified eco-evolutionary theory of biological organization.

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