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Opinion

Emergent feedback between symbiosis form and population dynamics

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Symbiotic relationships represent prolonged physical interactions between different species and include various forms such as mutualism, commensalism, exploitation, and competition. Here, we show that the form of symbiosis may change with the densities of the symbiotic partners as they influence the costs and benefits each species experiences. In turn, the form of symbiosis is expected to influence species persistence, population dynamics, and ultimately ecosystem stability. Based on this, we introduce the theoretical concept of a density–symbiosis feedback, where population densities affect the form of symbiosis, and symbiosis form in return affects population dynamics. This dynamic interplay calls for a re-evaluation of traditional ecological concepts and a framework considering the flexibility in symbiosis forms.

Highlights

Density–symbiosis feedback suggest that population densities and symbiosis forms continuously influence each other.

Density–symbiosis feedback requires a dynamic view of the costs and benefits associated with density-dependent symbiosis to fully understand ecological interactions and community stability.

The framework that recognizes the flexibility of symbiosis forms must extend beyond the focal symbiosis partners, considering the broader community context and abiotic changes in which these partners are embedded.

Shifts in symbiotic relationships

Symbiotic relationships – referring to the prolonged physical association of two or more different species [1] – are common across all ecosystems and can determine their dynamics and functioning, as demonstrated for example, in coral reefs [2], plant–pollinator networks [3], and stream communities [4]. Symbiotic interactions can take different forms, including **mutualism** (see Glossary), **commensalism**, **amensalism**, **exploitation**, and **competition**. The **symbiosis form** is specified by the underlying **costs** and **benefits** of the interaction for both partners, the relative duration of the association in relation to the species' generation times, and the dependence of the partners on each other (obligate or facultative) [5,6]; all depending on the biotic and abiotic context. A shift in the context can change the costs and benefits for the symbiosis partners such that the sign of the **net effect** (representing the difference between benefits and costs) of their interaction is altered, leading to a shift in the symbiosis form. Thus, it needs to be recognized that the form of symbioses may change along a continuum of species interactions and usually cannot be simply classified as a specific invariant relationship. This contrasts with almost all theories in ecology and evolution, used for example to predict population and community dynamics, which still assume species relationships to be invariant (but see [7–9]).

Shifts in the symbiosis form have been observed in laboratory and natural communities, often including interactions between two species within a broader community context, and resulting from individual or joint changes in biotic and abiotic conditions (Figure 1). For example, in the symbiosis between ants and aphids (Figure 1A), the sugar produced by aphids benefits ants, but the magnitude of the benefits varies with their relative densities, leading eventually to a shift from mutualism to commensalism [10]. Similarly, in interactions among four bacterial species whose growth is highly interdependent (Figure 1B), shifts in the resource environment (presence/absence of amino acids) can alter their symbiosis form, transitioning from mutualism to amensalism [11]. Food web theory focuses primarily on the strength of species interactions and their response to density-dependent effects and abiotic factors (Figure 1C), without considering potential shifts in

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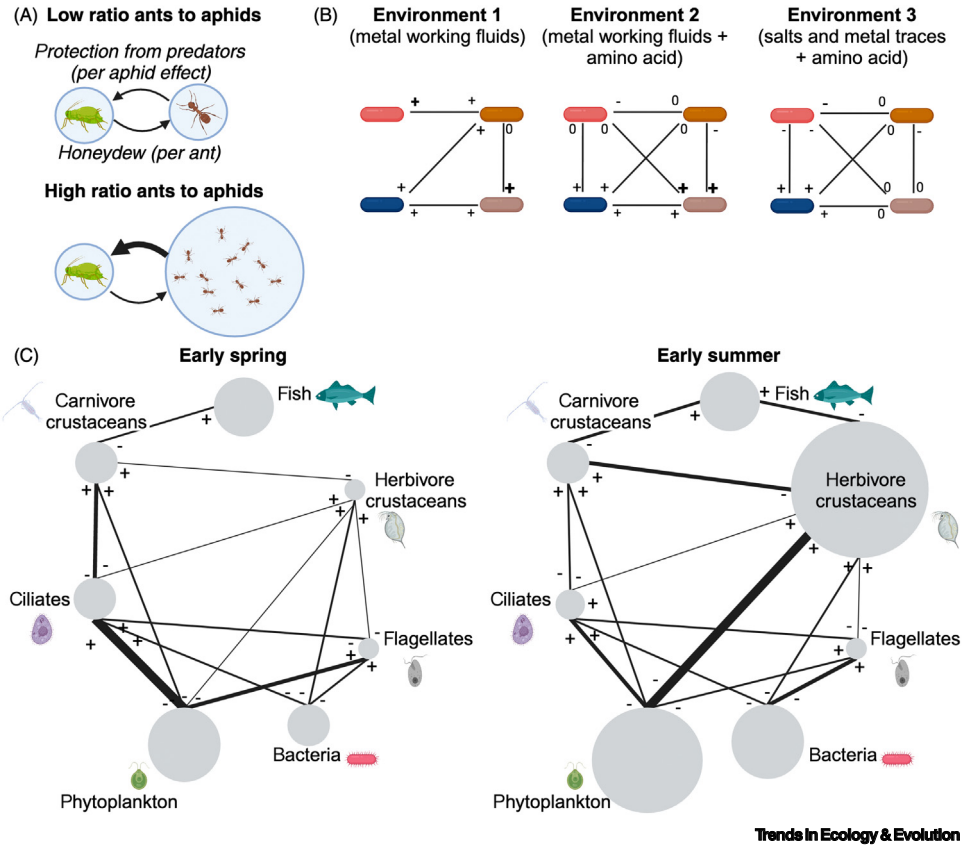

Figure 1. Context dependent shifts in symbiosis form and species interactions. (A) The symbiosis form in an ant–aphid relationship depends on the ant–aphid ratio. When this ratio increases, the amount of honeydew (sugar) provided by the aphids per ant decreases, eventually becoming too low to compensate for the protective benefits. This leads to a point where the growth of the aphid population stops first, followed by the cessation of ant growth, resulting in no further effect on either population and a shift from mutualism to commensalism or neutralism [10]. (B) In communities with four bacterial species, the form of symbiosis can shift between mutualistic, amensalistic, and exploitative interactions, depending on the environmental conditions in which the species grow. The net effects for each species are indicated next to the species as + (positive effect), - (negative effect), and no measurable effect (0), and the size of the symbols refers to the strength of the effect [11]. (C) The strength of trophic interactions (= exploitative shown as lines) in a lake varies with season and density of community members (size of circle represents the biomass, redrawn from [54]). While shifts in symbiosis form are not yet incorporated into food web theory, several studies have highlighted such shifts, including interactions between ciliates and phytoplankton [12,29] and herbivores and their microbes.

symbiosis form. However, recent studies suggest that symbiotic interactions within food webs may strongly be influenced by changes in densities, potentially altering the sign of the interaction between the focal symbiosis partners [12,13]. Thus, accounting for the context dependence of the form of symbiosis demands future theory development to facilitate a process-based understanding.

Symbiosis form is density dependent

Partner density is a major determinant of the form of symbiosis [12,14–19], for example, when symbiotic partners are rare or a poor match [20], or when other community members affect the interaction of the symbiosis. **Protective symbioses**, where symbionts protect hosts from the negative effects of parasites, can shift depending on parasite density. At high parasite densities, the symbiosis is mutualistic, with the benefits of protection outweighing the costs for the host. At low parasite densities, the symbiosis becomes commensalistic, with costs and benefits for the

Glossary

Amensalism: relationship between two species in which one species has a negative net effect while the effect on the other is neutral.
Benefits: advantages to one symbiosis partner resulting from the interaction with the other partner(s).
Costs: disadvantages to one symbiosis partner resulting from the interaction with the other partner(s).
Commensalism: relationship between two species in which one species has a positive net effect while the effect on the other is neutral.
Competition: relationship between two species in which both species have a negative net effect.
Density dependence: occurs when demographic rates (e.g., per capita growth or death rates) vary with the abundance of conspecific and/or heterospecific individuals from natural populations. Driver for regulation of population sizes.
Exploitation: general term describing the scenario where the net effect is positive for one interacting species (the exploiter) and negative for the other species (the victim). Exploiters can be parasites and predators.
Functional response: effect of density or trait of one species on demographic rates, fitness, or trait values of a second species.
Mutualism: relationship between two species in which both species have a positive net effect.
Net effect: sum of the costs and benefits.
Nutritional symbiosis: reciprocal exchange of metabolites that one partner has in excess and the other does not, and vice versa.
Phase plane: graphical representation that shows the trajectories of a dynamic system in 2D space, with each axis representing the size of a different population (or variable in general). It is used to analyze the stability and behavior of dynamical systems by showing how these variables interact and change over time.
Protective symbioses: symbionts protect hosts from negative effects of parasites or predators.
Symbiosis form: summary of the effects of the interaction among organisms that have positive, negative, or neutral effects on each other.

host resulting in no measurable net effect. In the absence of the parasite, the symbiosis shifts to parasitism, where the focal host provides resources to the symbiont without receiving any direct benefit [21]. For example, a microsporidian gut symbiont can affect how susceptible *Daphnia* are to infections by a fungal parasite. The overall net effect of the microsporidian symbiont for the *Daphnia* depends on the frequency of virulent parasites and availability of *Daphnia* resources [13]. Net effects for *Daphnia* are negative when resources and parasites are scarce and positive when parasites are common.

More broadly, and in line with a general definition for two interacting species [22], such **density dependencies** can be formulated as **functional responses** describing how the net effect of one species on another species changes with the density of the influencing species, ultimately influencing the strength (weak or strong) and sign (+, 0, –) of their interaction. Functional responses can take various forms including linear, saturating, or unimodal, depending on the response considered (e.g., growth rate, resource exchange rate, and level of protection against other parasites), and the biological details of the system. While the net effects of both partners are positive for mutualistic interactions (Figure 2A, left), they may saturate as the density of the partner increases (Figure 2A, second column). For exploitative interactions, the net effect is also

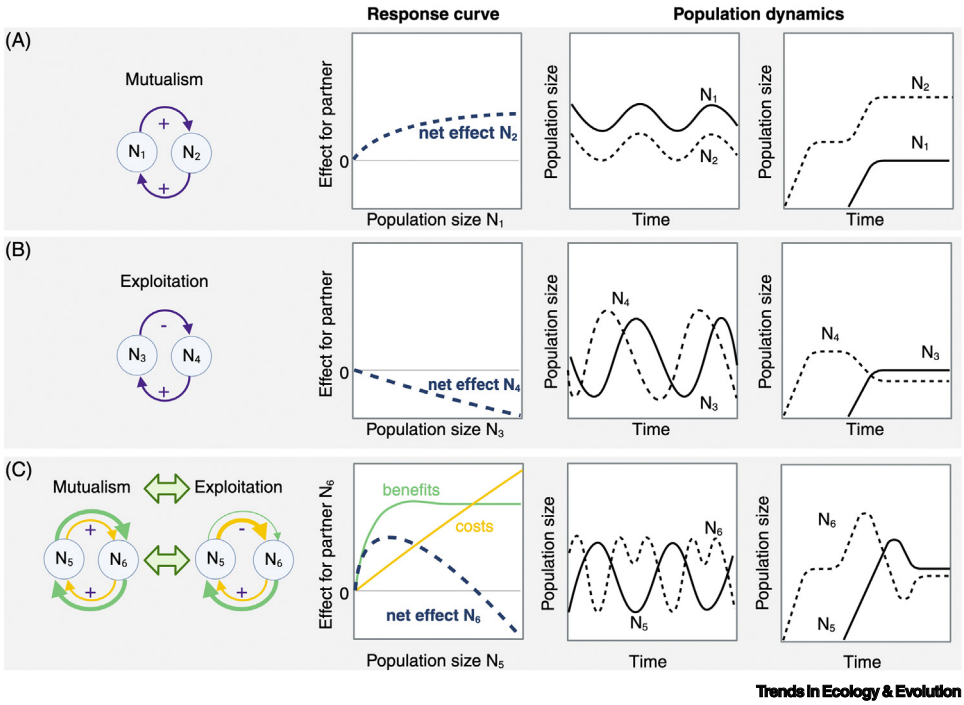

Figure 2. Context-independent and -dependent symbiosis forms and the resulting population dynamics. The classical ecological approach assumes a context-independent form of symbiosis [here mutualism (A) and exploitation (B)], where the sign of the net effect of the interaction does not change when the context changes (+/+ or +/- interactions; left column). Nevertheless, the magnitude of the net effect of one partner on the other can be density dependent (second column; for simplicity, only the effect for one partner is shown). This density dependence determines population dynamics, here synchronized cycles for mutualism (A) and a quarter phase-lagged cycles for exploitation (B) if populations N_1 or N_3 are driven by an external factor (third column). Another example of population dynamics is shown when N_1 (or N_3) is introduced into a system where N_2 (or N_4) has reached equilibrium (fourth column). (C) If the symbiosis form is density dependent, also the sign of the net effect changes with the context, which here is the density of one partner (i.e., N_5, shifts from mutualism to exploitation) and results from differences in density-dependent costs and benefits. The shift in symbiosis form can lead to distinct population dynamics when N_5 cycles through some external driver (third column), or when N_5 is introduced when population N_6 is at an equilibrium (fourth column).

positive for the exploiter but negative for the victim (Figure 2B, left). Both net effects are typically density dependent, with the functional response for the exploiter typically saturating as the victim density increases (Figure 2B, second column). Because functional responses capture the net density-dependent effects that species have on each other, they can be used to detect shifts in the form of symbiosis [23]. For example, if the net effect of the interaction shifts from positive to negative for the second species as the density of the first species increases (e.g., from a positive per capita growth rate for N_6 to a negative one with increasing density of N_5; Figure 2C, left and second column), the form of symbiosis shifts from mutualism to exploitation, assuming the net effect for the first species is always positive.

The processes driving the changes in the strength and sign of the net effects can be mechanistically understood from identifying the underlying costs and benefits of the interaction [22], which are themselves typically density-dependent. This implies that the sign of the net effect and thus the symbiosis form may change through altered costs and benefits [e.g., 17,18,20,24–27] (Figure 2C, left and middle). Such shifts in the form of symbiosis have been observed for example for **nutritional symbiosis** [28]. An important example is given by phototrophic *Chlorella* algae living inside ciliate hosts. While the endosymbiotic algae provide sugars to the ciliates, the ciliates provide mineral nutrients to the algae. A high density of endosymbionts is predicted to enhance competition for light and nutrients between the algal cells, lowering their photosynthetic rates. As the algal symbionts and the ciliate host share the photosynthetic products, the lower photosynthetic rates reduce the benefits for the host. The positive net effect for both partners at a lower endosymbiont density could thus shift to a negative net effect for the host when the sugars (benefit) provided by the endosymbionts decrease with increasing density of endosymbiotic algae while maintenance costs for the host remain high or even increase. Similarly, high ciliate densities may self-limit the host population as individuals compete for food. This reduces the amount of nutrients the ciliate can provide to the endosymbiotic algae, and thus their benefit, leading ultimately to a negative net effect for the algal symbionts as their costs remain unchanged [29,30], and thus a shift from mutualism to parasitism. Similar shifts in symbiosis form are found for protective symbioses, where the symbiosis form can shift between mutualism and parasitism [13,21,31]. For example, the protective benefits provided by ants to tree hoppers level off at high ant densities but costs continue to increase [32]. The studies described here and elsewhere [33,34] show that simple presence/absence manipulation of the symbiotic partners may often be insufficient to understand symbioses, and that testing for density-dependent net effects, costs and/or benefits is required [35,36].

Symbiosis form and population dynamics

Changes in population density can induce shifts in symbiosis form, but the symbiosis form also determines population dynamics over time through its direct effects on the species' per capita net growth rates. In a mutualistic system, both partners have positive effects on each other, leading to a self-enforcing positive feedback loop. This results in a principally unstable situation where the densities of both partners increase until at least one of them is limited either by an exogenous process (e.g., shading [37]) or is endogenously regulated (e.g., increased intraspecific competition). This may lead to synchronized population cycles or generally enhanced population sizes when growing together (Figure 2A, third and fourth columns). In contrast, exploitative systems represent a self-regulating negative feedback loop where the exploiter has a negative effect on victims' densities (Figure 1B, second column) and the victim has a positive effect on exploiter densities, which then feeds back to the victim. This may lead to population cycles or lower densities of the victims in the presence of the exploiter (Figure 2B, third and fourth columns [38]).

The causes and consequences of changes in population dynamics in general and in the context of symbiosis form shifts in particular can be derived from their functional responses [39]. They rely on the density-dependent costs and benefits of the symbiosis which determine population dynamics of the symbiosis partners through their effects on the species' per capita net growth rates [34]. First important insights from modeling work using consumer–resource interactions and density-dependent functional responses to describe benefits and costs showed that differential shifts in costs and benefits can change the parameter space where coexistence is possible [40,41]. For mutualistic interactions, different stability properties were found for linear, saturating, or unimodal functional responses [22]. Using information on costs and benefits in terms of resource consumption and supply by two mutualistic partners revealed intrinsically generated, time-delayed population cycles [42]; a dynamic pattern typically associated with exploitation in unstructured populations with trophic transfer [22,43]. Another example for dynamic patterns, which cannot be correctly interpreted by classical theory (e.g., mutualism or consumer–resource theory) may arise from shifts between exploitation and mutualism (Figure 2C). A major gap in the theory stems from the fact that it is unclear how current population dynamics theory applies in the presence of shifts in symbiosis form. Detailed consideration is needed of how the shapes of density-dependent costs and benefits can provide crucial information about population growth and limitation, conditions that stabilize or destabilize systems, and the resulting quantitative and qualitative dynamics (e.g., species persistence, food web structure, and energy transfer to higher trophic levels).

Density–symbiosis feedback

With density being the driver of shifts in symbiosis form and the symbiosis form affecting density changes, there is a potential for feedback between population density and the symbiosis form. This feedback may lead to continuous shifts in the symbiosis form driven by population density, while at the same time driving population density (Box 1). Such feedback may represent a general mechanism that regulates and potentially stabilizes the overall population dynamics of symbionts. For example, oversimplified models of mutualistic interactions that consider only positive feedback between population growth and density lead to unconstrained population growth in the absence of other species interactions that could constrain growth [44]. The addition of a mechanism that decreases the strength of the positive effects of mutualists with increasing population size generates a natural upper limit to the population size [45,46]. Such a mechanism may be the density–symbiosis feedback, where the interaction shifts to commensalism at high densities of one partner, but back to mutualism as the density of the partner decreases, eventually leading to zero population growth at the density at which the shift in symbiosis form occurs. For example, the density-dependent response in the ant–aphid system (Figure 1A) may prevent unlimited growth of aphids and ants by introducing an additional negative feedback loop, thus stabilizing it.

Density–symbiosis feedback can also lead to a full density–symbiosis feedback cycle, where symbiosis form and population sizes continuously change. For example, consider two symbionts N_5 and N_6 (Figure 2), where an increase in the density of N_5 causes a shift from positive to negative net effects of symbiont N_6 (e.g., from mutualism to exploitation), while the sign of the net effect of N_5 is independent of the density of N_6 (Figure 2C). Starting from low densities, the densities of both species will increase due to the positive net effects for both species, whereas at higher densities the density of N_6 will decrease due to the negative net effect of N_5 on N_6. The decline in the density of N_6 will reduce the benefit of species N_5 from N_6, so that N_5 also begins to decline. When species N_5 reaches a sufficiently low density, the net effect for species N_6 becomes positive again. Thus, the form of symbiosis changes from mutualism to exploitation and back again. If the net effect of both species on each other can shift from positive to negative values, the form of symbiosis can change between more than two different forms (see Figure II

Box 1. Density–symbiosis feedback

As an example, we describe density–symbiosis feedback for two species N_1 and N_2, each consuming one resource (N_1 -> R_1, N_2 -> R_2; Figure IA). The net effect (blue) of the interaction between N_1 and N_2 arises from the costs (orange) and benefits (green) the interaction has on each partner. We assume density-dependent costs and benefits, where for both partners benefits increase linearly, and costs increase non-linearly with increasing density (Figure IB).

$$\frac{dR_1}{dt} = (1-R_1)R_1 - \frac{a_1R_1}{1+a_1h_1R_1}N_1 \quad (1a)$$

$$\frac{dR_2}{dt} = (1-R_2)R_2 - \frac{a_2R_2}{1+a_2h_2R_2}N_2 \quad (1b)$$

$$\frac{dN_1}{dt} = \frac{a_1R_1}{1+a_1h_1R_1}N_1 - d_1N_1 - \boldsymbol{cN_2^2}N_1 + \boldsymbol{bN_2}N_1 \quad (1c)$$

$$\frac{dN_2}{dt} = \frac{a_2R_2}{1+a_2h_2R_2}N_2 - d_2N_2 - \boldsymbol{cN_1^2}N_2 + \boldsymbol{bN_1}N_2 \quad (1d)$$

Building upon an existing framework [43], our symbiosis model defined by eq. (1) extends classical consumer–resource models by explicitly describing costs and benefits of symbiotic interactions. Hence, our model assumes that the two resources R_1 and R_2 grow logistically in the absence of their consumers and that the consumers feed on their respective resource with a saturating (type II) functional response, which is specified by its attack rate *a* and handling time *h*. In the absence of the resources, the consumers N_1 and N_2 decline exponentially at a rate that is specified by their specific intrinsic mortality rate *d*. The population dynamics of the two consumers are further influenced by the costs and benefits that are inflicted by the other symbiosis partner. The density dependence of the costs is described by a parabolic function with acceleration cost parameter *c* and the density dependence of the benefits by a linear function with slope benefit parameter *b* (Figure IB).

The model results in continuous population cycles (Figure IIA), with costs and benefits also cycling (Figure IIB). Because the density dependence of costs and benefits differs for both species, the net effect (= sum of costs and benefits) for both species shifts from positive to negative with increasing density and back to positive with decreasing density (Figure IIC). The shifts in net effects do not occur for both species at the same time due to temporal differences in their population sizes leading to substantial differences in the emergent costs and benefits at a particular moment in time. As a result, the symbiosis form shifts from net positive and no effect (a) to net positive effects for both (b), to net positive and net negative effects (c).

The present modeling approach combines mechanistic and phenomenological frameworks, and is capable of modeling shifts in symbiosis form, using consumer–resource models that incorporate costs and benefits [42]. Such a shift in symbiosis form can also be captured in fully mechanistic models (see supplemental information online), which, for example, describe the interaction between aphids and ants in a community context, along with the density-dependent costs and benefits in greater detail. Importantly, the costs and benefits may arise from the exchange of resources, as well as from services such as protection against grazers. Future modeling approaches may also benefit from considering symbiosis form shifts through the lenses of higher-order interactions [55] and general niche theory [56].

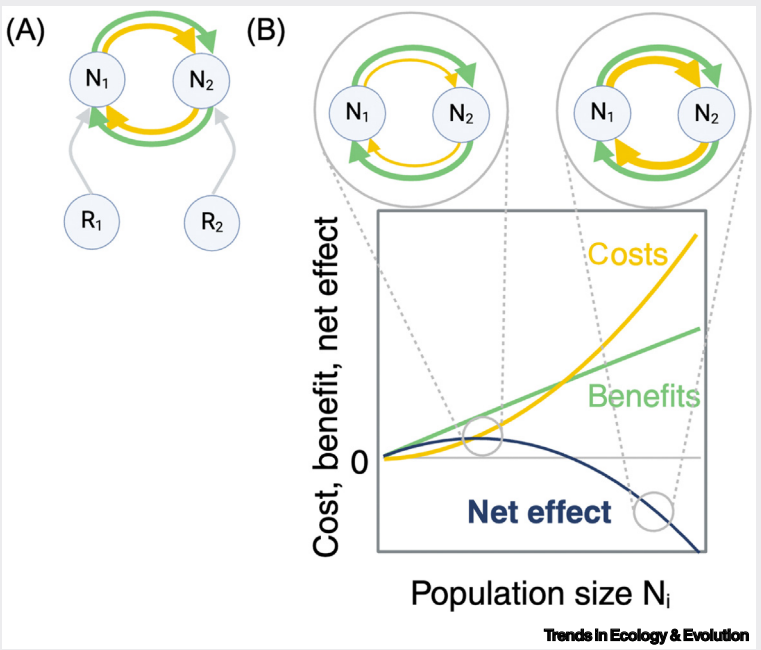

Figure I. Cost–benefit relationships in a general consumer–resource model. (A) Sketch of a consumer–resource system comprising two different consumers N_1 and N_2 that are feeding on two different resources R_1 and R_2, respectively. The two consumers directly interact with each other, providing benefits to one another but also inflicting costs on each other. (B) The costs, benefits and net effects of symbiosis are density dependent, and as the net effects shift between positive and negative values, the form of symbiosis itself is density dependent.

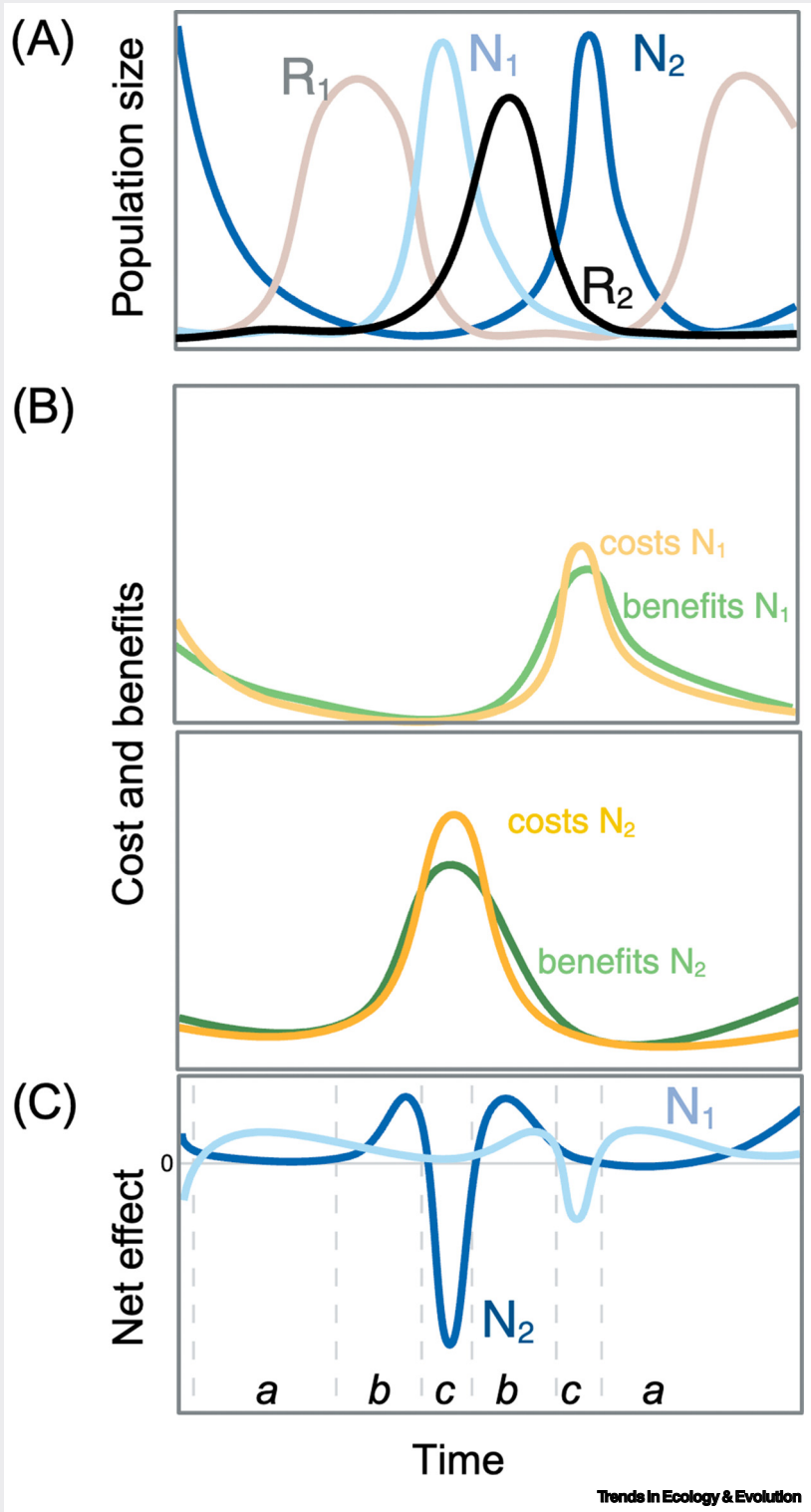

Figure II. Density–symbiosis feedback. (A) Temporal dynamics of consumer and resource population sizes N_1 (light blue), N_2 (dark blue) and R_1 and R_2 (grey and black), (B) costs (orange) and benefits (green) imposed on N_1 by N_2 respectively on N_2 by N_1 and (C) resulting net effects of the symbiosis for N_1 (light blue) and N_8 (dark blue). Symbiosis form commensalism (a), mutualism (b), and parasitism (c).

in Box 1). Thus, if the temporal changes in species densities and symbiosis form occur with a time lag for the two species, recurrent oscillations between species density and symbiosis form are inevitable, involving changes in the shape of population dynamics; for example, from population cycles towards steady state and back again. Consequently, empirical time series of population densities may be misinterpreted if potential density–symbiosis feedback is not considered (i.e., misinterpretation of the symbiosis form, or incorrect assumptions about the processes underlying population dynamics).

Density–symbiosis feedback and food webs

Such feedback dynamics between population density and symbiosis form have not been formally described, but they bear far-reaching consequences for food web dynamics, in addition to their effects on population dynamics. This is because individual symbioses are naturally embedded in a food web context and the form and strength of trophic links within food webs can significantly affect species diversity [47] and the biomass and production of different trophic levels [48]. For example, when species densities and their interactions influence the costs and benefits of a symbiotic relationship, they ultimately modulate the density-dependent effects one species has on another, thereby shaping the form of the symbiosis (e.g., protective symbiosis). An altered form of symbiosis, in turn, may feedback on the food web dynamics by changing the strength of trophic links and individual population dynamics (Figure 1C). For example, a reduction in the algal endosymbiont load of a ciliate host may lower the transfer efficiency to top consumers. This is because the many endosymbionts packed inside the ciliate serve as food for larger omnivores, which are suitable prey for fish. In contrast, the free-living algae can only be consumed by small herbivores which need to be repackaged by larger consumer to become suitable for fish. Moving from a static to a dynamic perspective of interactions within a food web by allowing for rewiring of the links, may greatly improve theoretical concepts and our understanding of empirical findings. It may provide important insights into the stability of communities, food web structure, and maintenance of biodiversity, given the many positive and negative feedback loops at different temporal scales within food webs (Figure 1C). We expect that the development of a theory on density–symbiosis feedback will have an impact similar to that of the development of the theory of eco-evolutionary dynamics [49]. Indeed, the density–symbiosis feedback has similarities to eco-evolutionary feedback where a property of the system (species traits) varies with the densities of the interacting species, while the densities themselves are a function of the property of the system [50–53].

Concluding remarks: going forward

The proposed concept of density–symbiosis feedback requires further development and integration into general concepts in ecology (see Outstanding questions). This remains challenging for at least two reasons. First, data to quantify density-dependent symbioses and how costs and benefits contribute to changes in symbiosis form are only available for a few systems yet (e.g., protective symbiosis of aphid–ant) but needed for a process-based understanding. Second, research on population and community dynamics needs to include density-dependent forms of symbiosis, moving beyond the assumption of static symbiosis forms and testing the regulatory consequences of density–symbiosis feedback. This requires time series of high-frequency measurements of population sizes over many generations to allow for the emergence of delayed responses in the form of symbioses and population dynamics, and thus for the feedback between symbiosis form and density to develop. It is essential to develop testable predictions regarding the positive and negative regulatory consequences of density–symbiosis feedback. Both empirical and theoretical work should prioritize generating and validating these predictions to understand how population and community dynamics differ when symbiotic forms can change, and density–symbiosis feedback is possible. To address these challenges, we can

Outstanding questions

Under what conditions are density–symbiosis feedback dynamics expected and what (unique) types of feedback dynamics emerge within different symbioses?

Are specific systems (e.g., terrestrial or aquatic communities) or types of symbiosis (e.g., protective or nutritional symbiosis) more likely to display density–symbiosis feedback?

Are there unique population dynamics that cannot be predicted with theory that does not take the density–symbiosis feedback into account?

Which types of functional responses most often describe the cost-benefit-relationships underlying symbiosis and which types of functional responses are most often involved in density–symbiosis feedback?

leverage existing experimental and modeling approaches (Box 2), as the related field of eco-evolutionary dynamics is rich in theoretical and empirical examples that provide valuable tools and frameworks for detecting and quantifying feedback impacts. Bringing up a concept of density–symbiosis feedback involves revisiting basic concepts in ecology, such as the forms of functional responses and their underlying mechanisms, the presence, amplitude and length (period) of population cycles, and phase relationships between oscillations in population sizes. By addressing these aspects, we can enhance our process-based understanding of various ecological phenomena.

Box 2. Proposed workflows for studying density–symbiosis feedback

Obtaining a process-based understanding of density–symbiosis feedback may require integration of different mathematical and experimental approaches.

1. Short-term experiments: conduct experiments to assess the costs and benefits of symbiosis by maintaining a constant density of one partner or accounting for its density changes during the experiment (as done, e.g., in measuring exploiter ingestion rates as a function of victim density [57]), while measuring the response of the other symbiotic partner (i.e., the cost or benefit). This allows for the separation of costs and benefits through comparative population growth studies, where conditions are manipulated to ensure that either costs or benefits are negligible [12] (e.g., limiting light in photosymbiosis, thus reducing the benefits to the heterotrophic partner). By fitting functional response curves to the data, we can identify critical population density thresholds that lead to changes in the form of symbiosis.
2. Dynamic modeling: utilize dynamical models based on, for example, differential equations that describe consumer–resource dynamics, to explore the feedback between population densities and the form of symbioses. The density dependence of symbiosis form can be: (i) incorporated phenomenologically into species growth equations using functional response terms that directly relate the densities of symbiotic partners to their corresponding per capita growth rates; (ii) into functional responses, which include associated costs and benefits; or (iii) mechanistically, depending on information available (e.g., obtained from short-term experiments). These models can then be used to predict various population dynamics, such as steady states or cyclic behaviors, based on different symbiosis forms and parameter ranges. They also help to identify conditions that promote density–symbiosis feedback dynamics and to inform corresponding experiments. This allows comparison of dynamics with and without density–symbiosis feedback.
3. Long-term experiments: implement long-term experiments to test the predictions from the model. In particular, compare the dynamical patterns in experiments that allow for density–symbiosis feedback with those that do not (Figure I). This analysis may include examining temporal means, variances, and covariance structures, as well as using spectral compositions (Fourier and Wavelet analysis) and reconstruction of **phase planes** (Figure I bottom). Key features to assess include the amplitudes and periods of population cycles, phase relationships (e.g., in-phase, out-of-phase, or quarter-phase shifts) and the occurrence of intermittent cycles between oscillating population dynamics. These comparisons can reveal quantitative differences in the dynamics [52] and in the attractor forms (e.g., ratios of the major and minor axes [53] or the existence of intersection points in the trajectory (Figure I, bottom row), thus indicating the type of symbiosis and the presence of a shift in symbiosis form.
4. Machine learning and statistical modeling: when direct experimental methods to establish functional responses and to manipulate symbiosis forms are not yet available (e.g., in complex interactions), advanced time series analysis tools can help to detect density–symbiosis feedback and their impacts on population dynamics involving uncovering the underlying drivers and processes behind shifts in symbiosis form. Promising tools include a mix of machine learning and statistical modeling approaches tailored to the specifics of the ecological data. For example, regression trees and recurrent neural networks (RNNs) [58,59] are promising tools that may help to identify the density-dependent net effects or cost–benefit relationships underlying potential shifts in symbiosis form.

In addition, utilizing statistical modeling may allow us to differentiate between various mechanisms giving rise to similar population dynamics, such as density–symbiosis feedback. For instance, intermittent cycles like those observed for the density–symbiosis feedback of N_5 and N_6 (see Figure 2C in main text) have also been noted in coevolving systems, where flexible species interactions arose from trait changes [60]. Using statistical modeling, alongside alternative hypothesis testing and comparisons to empirical time series of population densities, allows to test whether a model considering density–symbiosis feedback (e.g., the model for Figure 2C in main text) or a model considering coevolution are more likely to explain dynamics observed in experiments or the field [61]. Differentiating between the presence of various processes is a challenge, but one that is not fundamentally different from the broader challenge we face in understanding communities. We argue that incorporating the potential of the density–symbiosis feedback and its consequences offers a more nuanced and deeper understanding of the processes driving community dynamics.

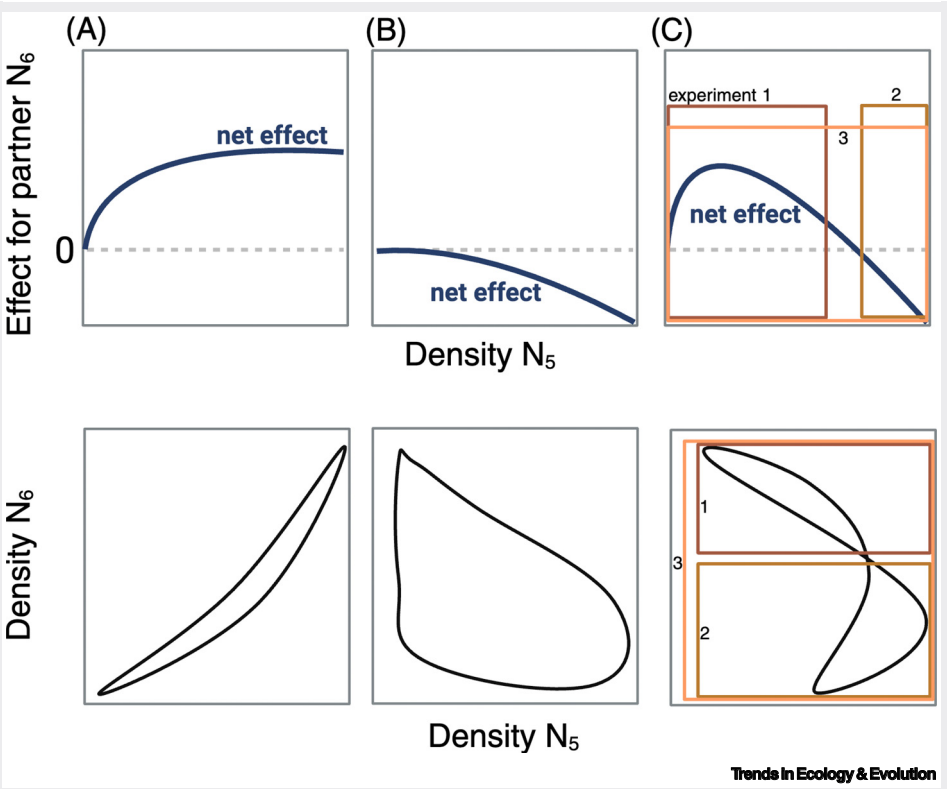

Figure I. Experimental and modeling approaches to test for density–symbiosis feedback. First, identify the environmental conditions (e.g., nutrient concentrations) where the functional response (top row) and the underlying costs and benefits (not shown for simplicity, but see Figure 2 in main text) of the symbiotic partners lead to a fixed form of symbiosis (A: mutualism, experiment 1; B: exploitation, experiment 2) or a shift (C: mutualism and exploitation, experiment 3). Second, perform experiments and/or simulations and follow the population dynamics (as in Figure 2 in main text), which can be further analyzed, for example, by constructing phase planes (bottom row). The population dynamics should then be compared between the scenarios with fixed symbioses form (A, B, experiment 1 and 2) and when the symbiosis form can shift (C, experiment 3).

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Declaration of interests

No interests are declared.

Supplemental information

Supplementary data to this article can be found online at https://doi.org/10.1016/j.tree.2025.02.006.

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