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The Evolution of Dependence and Cohesion in Incipient Endosymbioses

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ABSTRACT: Eukaryogenesis is the prototypical example of an egalitarian evolutionary transition in individuality, and endosymbiosis, more generally, is central to the origins of many complex biological systems. Why do only some symbioses undergo such a transition, and how does the host-symbiont relationship change during this process? Here, we characterize endosymbiosis by two emergent collective-level properties: host and symbiont survival as a collective ("mutual dependence") and the level of synchronized reproduction ("reproductive cohesion"). Using adaptive dynamics, we study the evolution of the traits underlying these properties. First, by adding a carrying capacity for the collective population—a realism omitted in previous models—we find novel reasons why complete dependence or cohesion might not evolve, thus providing further theoretical support for the rarity of transitions in individuality. Second, our model suggests that asymmetries in evolutionary outcomes of hosts and symbionts can be explained by a difference in their population growth parameters, coupled with their shared fate when in a collective. Last, we show that during the early stages of an endosymbiosis, even if investments in dependence and cohesion are uncorrelated, mutual dependence arises faster than reproductive cohesion. Our results hence shed light on three aspects of endosymbiosis: coevolution between the host and symbiont, coevolution between dependence and cohesion, and ultimately the opportunity to undergo an evolutionary transition. Connecting to ecological factors, this work uncovers fundamental properties of endosymbioses, providing a clear way forward for theoretical and empirical investigations.

Keywords: major evolutionary transitions, obligacy, mitochondria, microbiome, adaptive dynamics, Red King effect.

Introduction

Endosymbiosis is a phenomenon of central importance in evolutionary biology, leading to the origin of eukaryotes and several astonishing long-term associations between different species. It is the prototypical example of an egalitarian transition in individuality: initially, autonomous and unrelated entities—the host and symbiont—come together to give rise to a more complex, integrated entity (Szathmáry and Smith 1995; Queller 2000; Szathmáry 2015; West et al. 2015). The origin of endosymbiosis is not only a marked evolutionary transition but also a characteristic energy transition (Lane and Martin 2010). Arguably, access to more energy processing via the endosymbionts set the stage for further evolutionary leaps, such as multicellularity and beyond (Lane 2015).

Endosymbionts are present in most life forms, even in unicellular prokaryotes (Wujek 1979; Corsaro et al. 1999). Mitochondria have been famously shown to be endosymbionts arising from an ancient union between Archaeabacteria and an alphaproteobacterium (Sagan 1967; Koonin and Yutin 2014; Martijn et al. 2018; Fan et al. 2020). Many insects, such as the sap-sucking aphids, have been codiversifying with their *Buchnera*, *Wigglesworthia*, and *Wolbachia* endosymbionts for millions of years (Shigenobu et al. 2000; Wu et al. 2004; Zientz et al. 2004; Hansen and Moran 2011). There are examples from diverse ecologies across the globe—methanogenic endosymbionts in anaerobic ciliates (Embley and Finlay 1994), nitrogen-fixing endosymbionts in the diatom *Rhopalodia* (Prechtl et al. 2004), consortia of chemosynthetic bacteria in gutless tubeworms (Woyke et al. 2006), and cyanobacterial endosymbionts in sponges (Thacker 2005). New kinds of endosymbiotic associations continue being discovered, such as denitrifying

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endosymbionts in anaerobic ciliates (Graf et al. 2021). Despite this widespread prevalence, endosymbiosis and egalitarian evolutionary transitions are understudied relative to their fraternal counterparts, such as the evolution of multicellularity or eusociality (for which many review or book-length treatments exist; e.g., Hölldobler and Wilson 2008; Herron et al. 2022). However, this point of view is slowly changing with the recent emergence of more studies of symbiosis (Law and Dieckmann 1998; Estrela et al. 2016; Zachar and Szathmáry 2017; Zachar et al. 2018; Nguyen and van Baalen 2020; Patel and West 2022).

In this work, we are interested in the relationship between the host and symbiont and how it evolves throughout an evolutionary transition in individuality. By a transition in individuality, we mean the emergence—from individuals of one or more species that can undergo evolution—of a higher-level entity that can itself undergo Darwinian evolution. Transitions where the lower-level individuals making up a collective are unrelated are called "egalitarian" (Maynard Smith and Szathmáry 1995). Some symbioses have undergone such a transition, whereas others have not. For example, protomitochondria and their ancestral hosts underwent a transition to form the modern eukaryotic cell (Sagan 1967). *Buchnera* endosymbionts are obligately dependent on their aphid hosts, vertically transmitted, and have small genomes (Bennett and Moran 2015). On the other hand, while the tubeworm *Riftia* is obligately dependent on its symbiont *Endoriftia*, the latter has a free-living stage and is transmitted horizontally (Nussbaumer et al. 2006). Similarly, the bobtail squid *Euprymna scolopes* and its bioluminescent *Vibrio* symbiont are both facultative, and the symbiont is acquired horizontally every generation (McFall-Ngai 2014). What controls this difference in outcomes, and how is it impacted by the host's and symbiont's life history traits? How do the properties of the collective coevolve, and is there a difference between host and symbiont evolutionary trajectories? Such questions were introduced in the works of Law and Dieckmann (1998) and Nguyen and van Baalen (2020). These models emphasized different aspects of symbioses. Law and Dieckmann (1998) considered the evolution of an exploitative symbiont and showed that even unidirectional resource transfer can lead to an evolutionary transition. Nguyen and van Baalen (2020) considered a trade-off between independent reproduction and host encounter rate and showed that this can lead to evolutionary equilibria where the symbiont is facultatively dependent on its host. However, certain assumptions were made for analytical tractability, such as exponential population growth without any regulation for hosts, symbionts, or collectives (Law and Dieckmann 1998) and ignoring the evolution of host traits and letting collectives grow exponentially (Nguyen and van Baalen 2020). In this study, we, too, make a new simplifying assumption (see "An Eco-Evolutionary Model," parameter d), but it allows us to relax many others and, in doing so, ask a variety of different questions about host-symbiont coevolution with reasonable population dynamics.

To begin, we define a host-symbiont collective to be an obligate endosymbiosis if it exhibits three properties: (i) intracellular location of the symbiont; (ii) at least one of the host or symbiont is obligately dependent on this interaction; and (iii) the collective can reproduce synchronously (i.e., as a unit). Following Keeling and McCutcheon (2017), we use "symbiosis" to mean any sustained organismal interaction on the pathogenic-beneficial continuum. Synchronized collective reproduction, which is the target of our notion of "reproductive cohesion," is similar to, but stronger than, vertical symbiont transmission; we also include the requirement that the replication of the two partners is coupled, such as the coordination of mitochondrial fission and segregation with the cell cycle (although this is more complicated; see Mishra and Chan 2014). Importantly, synchronized reproduction endows the collective with a life cycle, previously proposed as the defining characteristic of an entity that can undergo an evolutionary transition (van Gestel and Tarnita 2017). For example, our definition excludes gut microbiomes, as there is no intracellular location or synchronized reproduction.

To study the conditions for the evolution of obligate endosymbiosis, we use evolutionary invasion analysis from the adaptive dynamics framework (Metz et al. 1992; Dieckmann and Law 1996; Geritz et al. 1998; Otto and Day 2007). This is a framework to study the long-term evolution by natural selection of traits that affect their bearer's ecological interactions. The evolutionary fate of new rare mutants is studied by determining whether they can invade and fix in the population in which they arise. This analysis assumes the separation of ecological and evolutionary timescales: the ecological processes dictating the fate of a mutant ("natural selection") take place much faster than the timescale in which new host/symbiont mutants arise.

An Eco-Evolutionary Model

We consider three populations—free-living hosts (H), free-living symbionts (S), and host-symbiont collectives (C). The primary process of interest is the evolution of the growth rates of these populations; we characterize obligate endosymbiosis by a positive growth rate for the collective and a zero growth rate for the free-living types.

Inspired by Estrela et al. (2016), we characterize a symbiosis by two emergent, collective-level quantities: the degree of host-symbiont mutual dependence and the degree of their reproductive cohesion (see fig. 1). Mutual dependence is an aggregative measure of how well the two

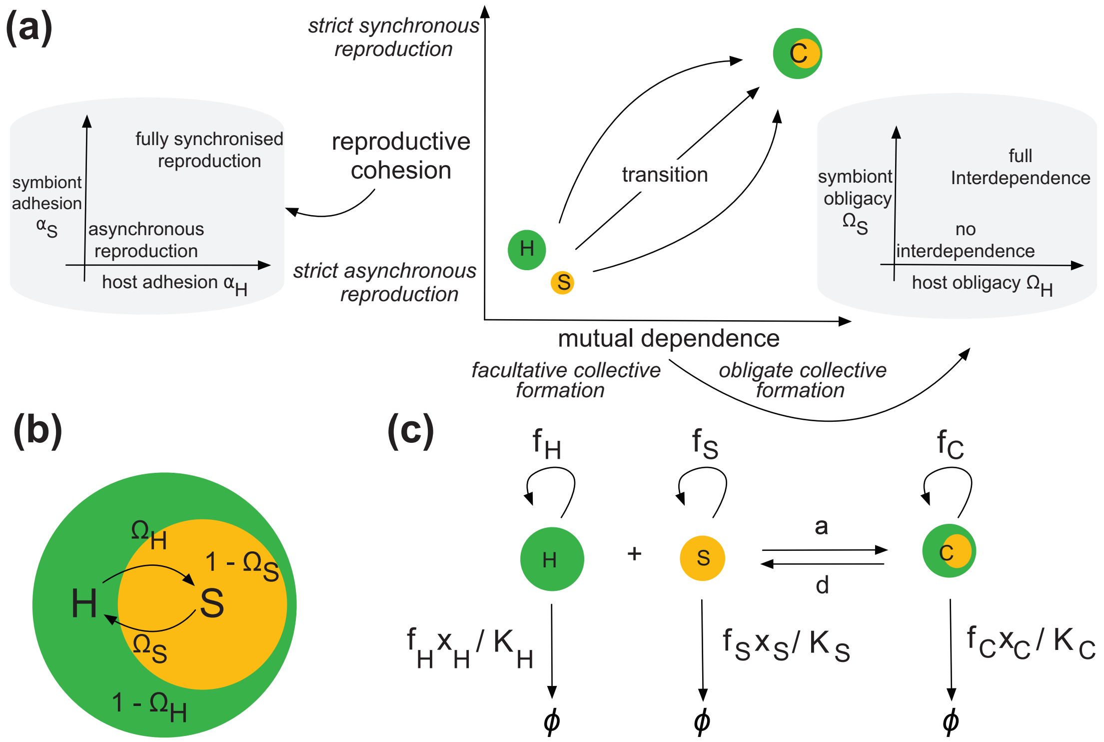

Figure 1: *a*, We conceptualize the trajectory of an evolutionary transition in the plane of two quantities—the reproductive cohesion of the lower-level individuals and the degree of mutual dependence between them. The adhesions α_H and α_S of the host and symbiont respectively control their investment in reproductive cohesion, that is, the degree of synchronized reproduction. The obligacy Ω_i describes the investment of type *i* in growth as a collective. *b*, On a microscopic scale, it is helpful to picture that there is—exclusively when they are both part of the collective—resource exchange between the host and symbiont. In this setting, the traits Ω_i control how much resource sharing the host/symbiont individuals are prone to. The trait α_i is more phenomenological and is most concretely connected to the magnitude of synchronized versus asynchronized reproduction of species *i*. *c*, Flows of the population dynamical model. All populations have a logistic growth rate corresponding, for example, to an intrinsic birth rate f_i and a density-dependent death rate $f_i x_i / K_i$. The host and symbiont associate and dissociate with rates *a* and *d*, respectively.

partners grow when free-living instead of when they are part of a collective; reproductive cohesion measures how often they reproduce synchronously instead of individually. The evolution of symbioses can thus be visualized as taking place in the plane of these two collective-level quantities. We say that an evolutionary transition in individuality occurs when there is complete mutual dependence and reproductive cohesion—the constituent individuals cannot live or reproduce without the other. We aim to understand the evolutionary trajectories in this dependence-cohesion plane.

To study the joint evolution of the traits underlying dependence and cohesion, we use the method of evolutionary invasion analysis. The main object of interest is the invasion fitness of a mutant in the environment generated by a resident population. It is assumed in this framework that the ecological and evolutionary timescales can be separated; that is, the (ecological) realization of a mutant's fate takes place much faster relative to the (evolutionary) timescale on which the next mutant arises (Metz et al. 1992).

We formalize the ecological (i.e., population) dynamics over short, mutation-free timescales as follows. Let f_H, f_S, and f_C be the growth rates of the host, symbiont, and collective populations, respectively. Furthermore, suppose the host and symbiont associate with and dissociate from each other at rates *a* and *d*, flowing into and out of the collective population. See figure 1*c* for a graphical representation of all possible events. The dynamics are given by

$$\begin{aligned} \dot{x}_H &= f_H x_H \left(1 - \frac{x_H}{K_H}\right) - a x_H x_S + d x_C, \\ \dot{x}_S &= f_S x_S \left(1 - \frac{x_S}{K_S}\right) - a x_H x_S + d x_C, \qquad (1) \\ \dot{x}_C &= f_C x_C \left(1 - \frac{x_C}{K_C}\right) + a x_H x_S - d x_C, \end{aligned}$$

where K_i is the carrying capacity of population i. These dynamics are our default model, which we study extensively. To achieve some analytical results, we will also study this model with an infinite collective carrying capacity ($K_C \to \infty$). We also explore numerically different extensions, which we specify in the respective results sections.

The parameters of the population dynamical model above depend on the traits underlying dependence and cohesion. Consider first mutual dependence: we introduce the traits Ω_H and Ω_S, referred to hereafter as the "obligacy" of the host and symbiont, respectively (fig. 1*a*). These are dimensionless numbers in $[0, 1]$ and denote the degree of dependence of the host and symbiont on the formation of the collectives. These traits formalize a trade-off between individual (f_H, f_S) and collective reproduction rate f_C. To make explicit the colocalized nature of an endosymbiotic interaction, we assume that the benefits of endosymbiosis are present only when the organisms are part of the collective, implying, for example, that the growth rates of the host population in isolation do not depend on the symbiont's investment (and vice versa).

With regard to reproductive cohesion, we introduce the traits α_H and α_S, hereafter referred to as the "adhesion" of the host and symbiont, respectively. These are also dimensionless in $[0, 1]$, and a higher adhesion denotes a higher association rate a, a lower dissociation d, and a higher propensity of synchronized birth f_C. These traits induce a trade-off between processes favoring the formation of the collective and those favoring the individuals. The mathematical translation of these statements is in terms of the partial derivatives of f_i, a, and d along the traits and is stated precisely in section S1.1 of the supplemental PDF. The mapping of traits to population dynamical parameters that we will use for most of this work is

$$
\begin{aligned}
f_H(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= r_H(1 - \Omega_H), \\
f_S(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= r_S(1 - \Omega_S), \\
f_C(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= r_C \Omega_H \Omega_S \alpha_H \alpha_S, \\
d(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= d_0(1 - \alpha_H \alpha_S), \\
a(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= a_0 \in \mathbb{R}_{\geq 0}.
\end{aligned}
\tag{2}
$$

The parameters in our model are summarized in table 1. In Results and Discussion," we present analyses of a set of interconnected versions of the model set up thus far. We first study the evolution of dependence only—letting obligacies Ω_i evolve while the adhesions α_i stay constant—and then vice versa (i.e., cohesion only). We then introduce a simplified version of the population dynamical equations (1) where the collective can grow exponentially; here we gain some analytical insights and study the joint evolution of obligacies and adhesions.

We assume a growth trade-off: that any investment in independent reproduction from either host or symbiont comes at a cost to their contribution to the collective growth rate (and vice versa). Notice that in equations (2), host independent growth rate f_H is maximum at $\Omega_H = 0$, decreases with increasing Ω_H, and is zero at $\Omega_H = 1$ (and identical for the symbiont). This trade-off is inspired by the consideration that the selective pressures while in a collective and those while free-living are sufficiently contrasting that mutations have antagonistic effects in these two niches. For example, endosymbiont adaptation can be influenced by external pH levels or ambient amino acid availability, which are plausibly vastly different inside and outside the host. Similar statements about nutritional availability or

Table 1: List of and associated information regarding all variables and parameters named in our model

Parameter	Description	Possible values	Comments
Ω_H, Ω_S	Host and symbiont obligacies	$[0, 1]$	Initially set to $(0, 0)$
α_H, α_S	Host and symbiont adhesions	$[0, 1]$	Initially set to $(0, 0)$
x_H, x_S, x_C	Population densities of host, symbiont, and collectives	$[0, \infty)$	Equilibrium densities depend on trait values
f_H, f_S, f_C	Growth rates of *H*, *S*, and *C* populations	$[0, \infty)$	Usually set such that $f_S > f_C > f_H$
K_H, K_S, K_C	Carrying capacities of *H*, *S*, and *C* populations	$[0, \infty)$	Usually set such that $K_S > K_C > K_H$
a, d	Association and dissociation rates	$[0, \infty)$	Initial $d >$ initial a
d_H, d_S	Within-collective mortality rates of host and symbionts	$[0, \infty)$	Assumed to not depend on any traits
b_H, b_S	Within-collective birth rates of host and symbionts	$[0, \infty)$	Assumed to not depend on any traits
r_H, r_S, r_C	Maximum values of f_H, f_S, and f_C	$[0, \infty)$	Only relevant when Ω_i and/or α_i are evolving
d_0	Maximum value of d	$[0, \infty)$	Only relevant when α_i are evolving

pathogen defense can also be made for the pressures on host adaptation. Such trade-offs have been observed in the squid-*Vibrio* symbiosis (Pankey et al. 2017; Cohen et al. 2020) and in some experiments with *Bradyrhizobium* symbionts of plants (Sachs et al. 2011; for a more extensive discussion of growth trade-offs, see Brockhurst et al. 2024). We are in this study interested primarily in mutualistic endosymbiosis, where increased investment from either partner increases the collective growth rate. The trade-off above is a case where investment into collective growth is a priori difficult to emerge because of the linked cost to free-living growth. It is possible that only the symbiont experiences such a trade-off or that there are mutations that only advantage the collective or disadvantage the free-living host/symbiont; we do not consider these in our model.

To differentiate between the Ω and α trait pairs, it is useful to focus on an example such as a fig-wasp mutualism (reviewed in Herre et al. 2008). This association is an enmeshing of two life cycles—the fig tree depends on the wasp, the pollinator; and the wasp is dependent on the fig tree (the fruit, to be specific) to complete a part of its development. Therefore, the two species are highly dependent on each other, but they do not physically reproduce as a unit. Hence, here the obligacies Ω_i are high, but the adhesions α_i are not.

Evolutionary invasion analysis. To compute an arbitrary mutant's invasion fitness, we suppose a resident population is at ecological equilibrium, that is, a stable steady state of the population dynamics (in our case, eqq. [1]). The abundances at this steady state are computed numerically, unless mentioned otherwise. It is assumed that a mutant then arises, with trait value drawn from a symmetric probability distribution centered at the resident trait. The fate of this mutant is decided via its invasion fitness, that is, the growth rate of a small number of mutants in the resident population (Metz et al. 1992). The mutant can invade if its invasion fitness is positive; if it is negative, the mutant becomes extinct (Dieckmann and Law 1996; Dercole and Rinaldi 2008). This quantity is traditionally defined as the largest eigenvalue of the Jacobian of equations (1) when augmented for the presence of a mutant type. However, in our case this quantity is not amenable to mathematical analysis, so we use the next-generation theorem, which gives an alternate characterization of the same number (van den Driessche and Watmough 2002; Hurford et al. 2010). We then use the canonical equation of adaptive dynamics (Dieckmann and Law 1996) to study the macroscopic behavior of long-term evolutionary trajectories (supplemental PDF, sec. S4).

Results and Discussion

In the first subsection, we investigate the case where obligacies evolve independently of the adhesions and vice versa. In the second subsection, we analyze an extension of the model that includes within-collective birth and death rates. Then, in the third subsection, we study the relative importance of the collective population's growth rate and carrying capacity in deciding the course of evolution. Finally, in the last subsection, we study obligacy and adhesion coevolution in a model more amenable to analytics, which we derive by assuming an infinitely large collective carrying capacity in equations (1).

It is challenging to analytically solve the system of equations (1) to determine the fixed points and their stability. However, we determined computationally that for a wide range of parameter values, the dynamics converges to a stable fixed point over the evolutionary change in our traits of interest (see the supplemental PDF, sec. S2.1). Moreover, the values of the equilibrium population sizes increase or decrease gradually with the trait values, suggesting that there is a single internal fixed point. We will assume throughout that $K_S > K_H$ and $r_S > r_H$, that is, the symbiont population has a higher carrying capacity and reaches it faster than the host. Consequently, on average over a given duration of time, more symbiont mutants arise than host mutants, and the symbiont trait hence has a higher rate of evolution (assuming, as we do, that the rate of mutation and the variance in the mutant trait distribution are the same for host and symbiont traits; see eq. [4.12] in Dieckmann and Law 1996).

Independent Evolution of Obligacies and Adhesions

We begin by understanding the evolution of the obligacies when adhesions are kept constant and vice versa. The mapping of obligacies to population dynamical parameters we use in figure 2*a*–2*c* is

$$\begin{aligned} f_H(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= r_H(1 - \Omega_H), \\ f_S(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= r_S(1 - \Omega_S), \\ f_C(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= r_C \Omega_H \Omega_S, \end{aligned} \tag{3}$$

where we assume that the adhesions α_i are not under selection. The constants r_H, r_S, and r_C set the scale of the parameters f_i; concretely, they can be understood as the intrinsic growth rates of the populations at either $\Omega_i = 0$ (for f_H and f_S) or when both obligacies are equal to 1 (for f_C). In figure 2*d*–2*f*, we assume obligacies to be constant and model the ecological consequences of a different adhesion via

$$\begin{aligned} f_C(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= r_C \alpha_H \alpha_S, \\ d(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= d_0(1 - \alpha_H \alpha_S), \\ a(\Omega_H, \alpha_H, \Omega_S, \alpha_S) &= a_0 \in \mathbb{R}_{\geq 0}. \end{aligned} \tag{4}$$

The constants r_C, d_0, and a_0 are again the maximum values of the respective functions and set the scale of variation.

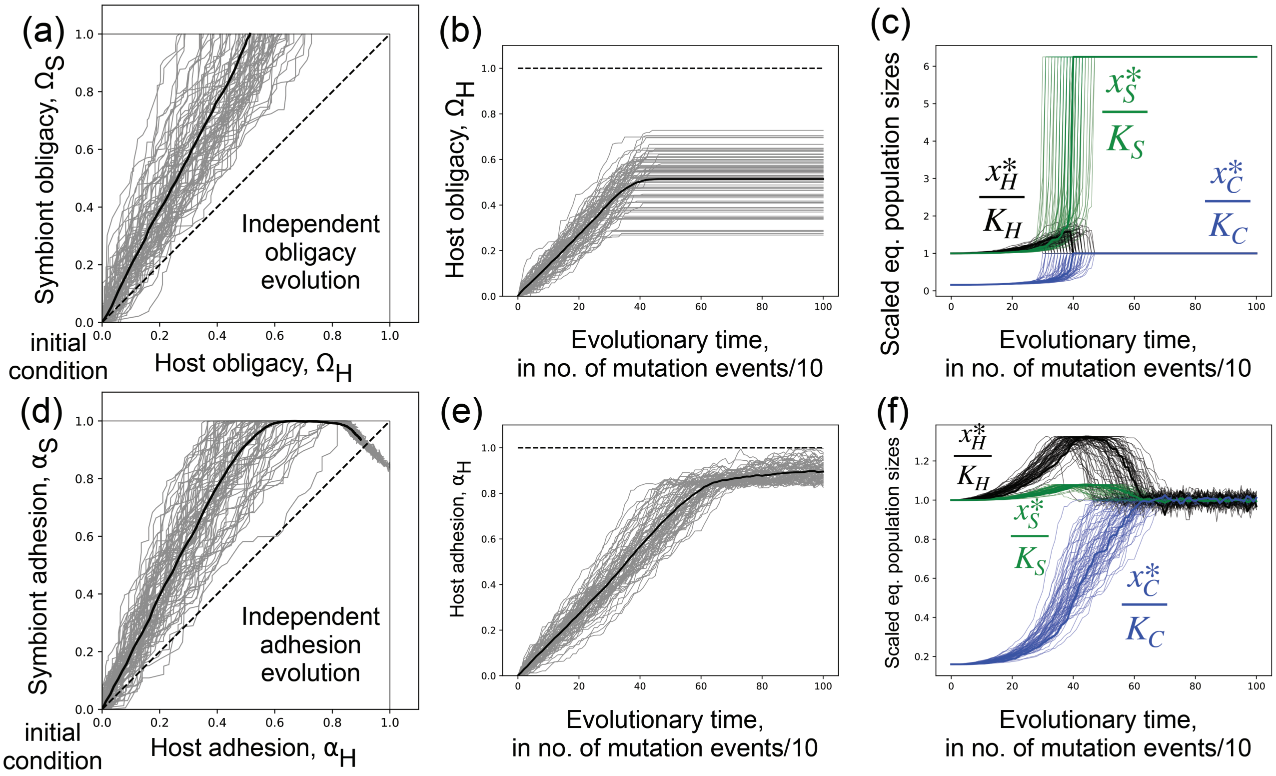

Figure 2: Evolutionary dynamics of host and symbiont obligacies. All panels contain results of 75 independent stochastic simulations. *a*, Symbiont obligacy evolves to 1, and then host obligacy is no longer under selection (see main text for an explanation). *b*, Symbiont adhesion evolves to 1, and then host adhesion increases until a certain value. The traits together then vary along a neutral ridge around (1, 1) (see main text for an explanation). *c*, *d*, These panels show the evolutionary trajectory of the host trait, since it is here that the nontrivial outcomes take place. Ω_H plateaus at different values based on when the value of Ω_S reaches 1. α_H increases up to a high value and stays close to it. Parameter values: for all, $K_H = 100$, $K_S = 200$, $K_C = 250$, $a_0 = 0.1$; for *a*, $r_H = 8$, $r_S = 20$, $r_C = 10$, $d = 50.0$; for *b* and *c*, $f_H = 8$, $f_S = 20$, $r_C = 10$, $d = 50$.

Results are presented in figure 2. First consider the evolutionary trajectory of the obligacies ($\Omega_H(t)$, $\Omega_S(t)$): the symbiont obligacy Ω_S reaches 1 first (denote this time by $t^*_{\Omega_S}$), and after this the selective pressure on Ω_H disappears, leading to stagnation in its value (fig. 2*a*, 2*b*). This lack of selection after $\Omega_S = 1$ occurs because when $f_S = 0$ (no independent symbiont reproduction), the host and collective populations equilibrate to their carrying capacities irrespective of Ω_H; the symbiont population is sustained only through dissociation (see eqq. [1]). However, the symbiont has a higher equilibrium population size when $\Omega_S = 1$ than when $\Omega_S < 1$ because of the "backflow" from the dissociation of the collectives (see the supplemental PDF, sec. S2.1, or eqq. [1]). The converse is valid for the host—its population size is not at the maximum possible over the trait space, while $\Omega_H < 1$. This is a counterintuitive result: the symbiont foregoes its ability to reproduce independently and has a higher equilibrium population size than its carrying capacity; the host now has a population size exactly equal to its carrying capacity (when it could be higher, i.e., at $\Omega_H = 1$) but retains its ability to reproduce independently (fig. 2*c*). Indeed, it is better (in terms of abundance) for both the host and the symbiont to give up independent reproduction and be sustained only through dissociation, but the faster-evolving population can do this first.

The above argument can also be made analytically via the computation of the basic reproductive number of a mutant $R_0(\tilde{\Omega}_H, \Omega_H, \Omega_S)$, which denotes (roughly) the number of offspring left by a mutant host with obligacy $\tilde{\Omega}_H$ that arises in a resident population of hosts with obligacy Ω_H and symbionts with obligacy Ω_S (derived using the next-generation theorem; see the supplemental PDF, sec. S4.1). This quantity is given by

$$R_0(\tilde{\Omega}_H, \Omega_H, \Omega_S) = \frac{\tilde{f}_H + \dfrac{d a x_S^*}{(d - \tilde{f}_C) + \tilde{f}_C \dfrac{x_C^*}{K_C}}}{\tilde{f}_H \dfrac{x_H^*}{K_H} + a x_S^*}, \qquad (5)$$

where an asterisk denotes that the value at equilibrium must be used. The R_0 is not maximally informative in our case, since we cannot analytically solve for the equilibrium population abundances x_i^*. Nevertheless, it can be shown (see the supplemental PDF, sec. S.4.1) that $R_0(\tilde{\Omega}_H, \Omega_H, 1) = 1$ for any combination $(\tilde{\Omega}_H, \Omega_H) \in (0,1]^2$—that is, there is no fitness difference between any Ω_H mutants that arise in the background of $\Omega_S = 1$. A consequence of this result that cannot be captured by adaptive dynamics is that this model predicts the accumulation of neutral genetic variation in the host population at loci coding for obligacy.

Now consider the evolutionary trajectory of adhesions, presented in figure 2*d* and 2*e*. Symbiont adhesion α_S reaches 1 first, while α_H is still smaller than 1, and then host adhesion increases until an evolutionarily stable strategy (ESS) is reached. Trajectories then drift along a curve near $(1,1)$. This ridge connects the states $(\Omega_H < 1, \Omega_S = 1)$ and $(\Omega_H = 1, \Omega_S < 1)$, and it is possible that a small proportion of trajectories eventually reaches $\Omega_H = 1$. The drift in figure 2*d*–*f* is what our model predicts of biological populations. However, its source in this figure is different: accepting false positives when deciding the fate of mutants based on $R_0 > 1$, which arise due to floating point errors that we cannot entirely remove. All neutral mutations would have $R_0 = 1$, whereas we accept values only larger than a value that is infinitesimally larger than 1 to exclude such errors (see associated scripts for exact details).

Nevertheless, there are two facts to explain: that the traits increase and that there is a host-symbiont asymmetry in outcomes. Our observations can be explained by the variation in equilibrium population sizes as traits change (for heatmaps, see the supplemental PDF, sec. S2.1). Notably, (i) they increase along the adhesions α_i (and hence the traits themselves also increase), and (ii) they do so nonmonotonically, with a local maximum in $x_i^*(\alpha_H, \alpha_S)$ occurring over a ridge in the interior of the $\alpha_H - \alpha_S$ space that surrounds the top right corner $(1,1)$ (see fig. S2; figs. S1–S14 are available online). The first consequence is that any trajectory (α_H, α_S) must pass over this ridge to reach $(1,1)$. The symbiont adhesion can reach 1 before encountering this bump because of its faster rate of change, and the trajectory has to overcome it then while α_H is still less than 1. This is the source of the asymmetry: if both species have the same r and K, then the landscape of x_i^* is the same, but now the trajectory (α_H, α_S) hits the ridge when both adhesions are approximately equal and less than 1 (see the supplemental PDF, sec. S3.1). We suggest that the inflection point of this local maximum corresponds to the ESS, since decreasing population size (even locally) is disadvantageous, and such a mutant could not invade.

More proximately, an increased adhesion leads to modifications in two forces acting on host/symbiont population size via the term dx_C: (1) a decrease because fewer dissociations occur but also (2) an increase because an increased adhesion increases f_C and, hence, the collective population size. Since we begin with the intuitive scenario of high dissociation rate and zero synchronized growth, an initial increase in adhesion is beneficial, but this benefit occurs only up to a point, after which the decrease in d overpowers the increase due to f_C. This switch is the explanation for the presence of the intermediate ESS and the ridges in population size curves. This demonstrates that it is essential to consider not only intuitive parameters like f_H or f_S but also population size dynamics, which can strongly influence invasion fitness in this context.

The Effect of Within-Collective Mortality and Reproduction

In our model, we have assumed so far that dissociation is perfect: all events producing free-living individuals from a collective give rise exactly to one host and one symbiont. However, it is likely that there is differential mortality for hosts and symbionts while they are in a collective or during dissociation. This would give rise to free-living hosts when the symbiont dies (at some rate d_S) and free-living symbionts with an analogous rate d_H. Furthermore, hosts and symbionts, while in a collective, can also give birth to free-living hosts or symbionts. Suppose this takes place at rates b_H and b_S, respectively. The population dynamics is then described by

$$\dot{x}_H = f_H x_H \left(1 - \frac{x_H}{K_H}\right) - a x_H x_S + d x_C + (d_S + b_H) x_C,$$

$$\dot{x}_S = f_S x_S \left(1 - \frac{x_S}{K_S}\right) - a x_H x_S + d x_C + (d_H + b_S) x_C, \quad (6)$$

$$\dot{x}_C = f_C x_C \left(1 - \frac{x_C}{K_C}\right) + a x_H x_S - d x_C - (d_S + d_H) x_C.$$

The previous section then corresponds to, for example, setting the rates $b_i = 0$ and $d_i = 0$, $i \in \{H, S\}$. The correspondence is slightly more general; one obtains equations (1) whenever $b_i = d_j$ for all combinations of $i, j \in \{H, S\}$, with the caveat that the corresponding value of the dissociation rate would be higher (i.e., $d + b_i + d_j$).

We consider two scenarios: (i) differential mortality while in a collective, but no within-collective reproduction ($d_H = d_S \neq 0$, $b_i = 0$, $i \in \{H, S\}$; fig. 3, *right*) and (ii) within-collective H (or S) can give birth to free-living H (or S) but within-collective mortality is absent ($b_H = b_S \neq 0, d_i = 0, i \in \{H, S\}$; fig. 3, *left*). For the sake of brevity, we do not consider the cases where $b_H \neq b_S$, where $d_H \neq d_S$, or where the within-collective birth and death rates are both greater than zero. However, the latter

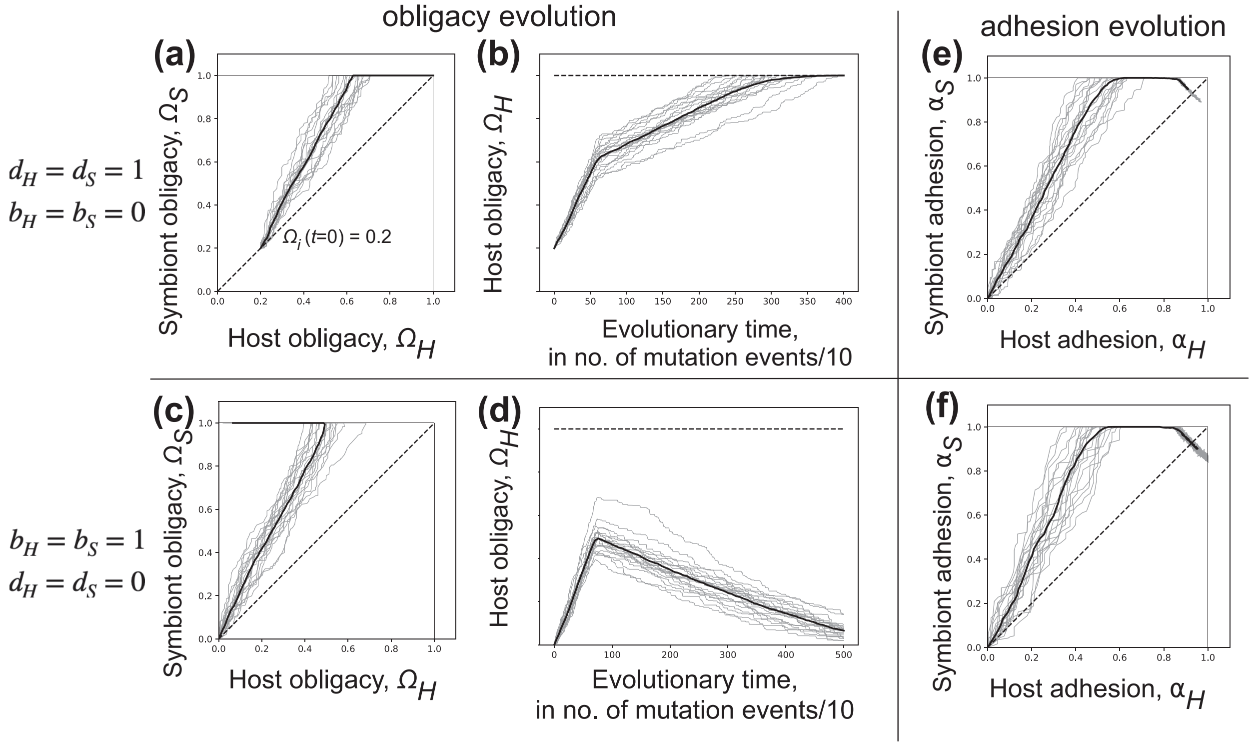

Figure 3: Evolutionary dynamics of obligacies and adhesions when b_i and d_i are nonzero. All panels contain results of 20 independent stochastic simulations. *a*, *b*, When $d_H = d_S > 0$, the initial obligacies must be above a threshold for them to further increase. Symbiont obligacy increases faster, and when Ω_S hits 1, host obligacy increases further up to 1. *c*, *d*, When $b_H = b_S > 0$, dependence directly increases over time without a threshold minimum value that is necessary; when Ω_S hits 1, host obligacy now decreases to zero. *e*, *f*, Qualitatively identical to adhesion evolution presented in figure 2. Parameter values: for all, $K_H = 100$, $K_S = 200$, $K_C = 250$, $a_0 = 0.1$; for *a*, *b*, *e*, $d_H = d_S = 1$, $b_H = b_S = 0$; for *c*, *d*, *f*, $d_H = d_S = 0$, $b_H = b_S = 1$; for *a*–*d*, $r_H = 8$, $r_S = 20$, $r_C = 10$, $d = 50.0$; for *e*, *f*, $f_H = 8$, $f_S = 20$, $r_C = 10$, $d_0 = 50$.

is not modeling a completely new phenomenon, since d_i and b_j appear together as an aggregate coefficient of the collective abundance x_C in equations (6).

First, the adhesion trajectories (fig. 3, *right*): there are no qualitative changes compared with the case when $d_i = b_i = 0$, and the prediction that the adhesions increase and then hit a ridge of ESSs is robust to the addition of the above within-collective rates. At higher shared values of d_i, the adhesions do not increase from initial values (see the supplemental PDF, sec. S3.4).

The evolution of obligacies, however, displays departures when $d_i > 0$ or when $b_i > 0$. When hosts or symbionts can die while in a collective but cannot give birth, the obligacies do not initially increase from $(0, 0)$ at all. However, if the obligacies are at a high enough initial value to begin with, the obligacies then increase as before, with the symbiont obligacy Ω_S reaching 1 first. This threshold initial value increases with the shared value of d_H and d_S, but above this value the dynamics proceed similarly to the earlier model (see the supplemental PDF, sec. S3.4), with one important difference: once $\Omega_S = 1$, the selective pressure on Ω_H does not disappear, and instead the host obligacy now also increases to 1, leading to full mutual dependence. At the state $\Omega_H = \Omega_S = 1$, the equilibrium population abundances remain at steady, nonzero values in the case of $d_S = d_H$.

When hosts and symbionts can give birth while in a collective but cannot die, the outcome is again different: the obligacies directly increase from $(0, 0)$ without needing a threshold dependence, but once symbiont obligacy reaches 1, the host is under selection to now decrease its obligacy. This leads to a nonmonotonic route to a one-sided mutualism, where the symbiont is completely dependent and the host not at all. In the ultimate state of $\Omega_H = 0$, $\Omega_S = 1$, there is no fixed point possible for equations (6); the symbiont becomes extinct, while the host and collective populations blow up because of the birth rates. At higher shared values of b_i, the obligacies still increase, but host-symbiont symmetry in obligacies is reduced (see the supplemental PDF, sec. S3.4).

To explain the above results, we again appeal to the population sizes at equilibrium. It can be shown that if

$d_S + b_H = d_H + b_S$ (which is true in fig. 3 by the parameters we have set), once $\Omega_S = 1$ (implying $f_S = 0$), the equilibrium abundances calculated from equations (6) are given by the equations

$$\begin{aligned} x_H^* &= K_H, \\ x_C^* &= \left(1 + \frac{(b_S - d_S)}{f_C}\right) K_C, \\ x_S^* &= \frac{(d + d_H + b_S) x_C^*}{a x_H^*}. \end{aligned} \tag{7}$$

Dependence on Ω_i here enters through the f_C in x_C^*: when $b_S > d_S$, an increased host obligacy decreases collective abundance at equilibrium x_C^*, and when $b_S < d_S$, an increased host obligacy increases x_C^*. More generally, the form of x_C^* reflects that the forces driving the collective population away from its carrying capacity are b_S-produced free-living symbionts that form collectives via host association and collectives leaving the compartment at rate d_S to form hosts. This suggests that even if the rates b_i and d_i are unequal, a case we have not tested here, the difference $b_S - d_S$ plays a central, if not solitary, role in deciding the outcome.

The inclusion of births and deaths of hosts and symbionts while in a collective therefore affects two properties of the trajectory: initial increase of the obligacies and what happens when $\Omega_S = 1$ is reached (see table 2 for a summary of these effects). Including trait dependence in these within-collective rates would further complicate the picture, since their values would become dynamic and combinations of the above arguments might become necessary. We do not consider this possibility here, but some possible consequences are discussed in “Conclusions and Conjectures.”

Having clarified the effects of the parameters b_i and d_i, we shall set them again to zero for the remaining sections to emphasize other predictions of this model.

Collective Growth Rate and Collective Carrying Capacity Have Different Effects on Evolutionary Outcomes

We have shown that dependence and cohesion can, in fact, increase under our assumptions and that associating with a partner to form a collective is thus beneficial. However, this benefit is in terms of two independent (at least in our model) parameters—the collective population’s growth rate r_C and its carrying capacity K_C. In this section, we are interested in which of these parameters is more important in determining the evolutionary outcome.

We computed evolutionary trajectories for high and low values of the parameters r_C and K_C each—$r_C \in \{1, 40\}$ and $K_C \in \{10, 500\}$. At the low value of K_C, both obligacies and adhesions remained at their initial condition $(0, 0)$; at the high value of K_C, they evolved away from $(0, 0)$. The outcome was not influenced by the value of r_C. This shows that it is more important that the collective’s equilibrium population size is high, no matter how much the mutant and resident differ in how fast they reach this size. We propose a cutoff for the threshold value of K_C in the following paragraphs.

Nevertheless, once K_C is high enough, its precise value can influence the ultimate values of adhesion but not obligacy. Figure 4 presents the results of evaluating the evolutionary trajectories of obligacies and adhesions at

Table 2: Summary of evolutionary outcomes for Ω_i and α_i depending on the rates of within-collective mortality and reproduction

Scenario	Parameters	Consequences on $\Omega_i(t)$	Consequences on $\alpha_i(t)$
Perfect collective dissociation, no within-collective births or deaths	$d_H = 0$, $d_S = 0$, $b_H = b_S = 0$	Both increase; host obligacy stagnates once symbiont is completely obligate	Increase, then drift along a ridge
Within-collective mortality, but no births	$d_H = d_S > 0$, $b_H = 0$, $b_S = 0$	Both increase if initial obligacy is high enough; ultimately, both host and symbiont become obligately dependent	Increase, then drift along a ridge
Within-collective hosts can give birth to new hosts (similarly symbionts), but no within-collective deaths	$b_H = b_S > 0$, $d_H = 0$, $d_S = 0$	Both increase without a threshold; ultimately, symbiont becomes fully obligate whereas host becomes completely independent	Increase, then drift along a ridge
Within-collective birth and death rates are all equal	$b_H = b_S = d_H = d_S$	Equivalent to setting $b_i = d_i = 0$ and increasing d, so there is no formal difference from the first row	

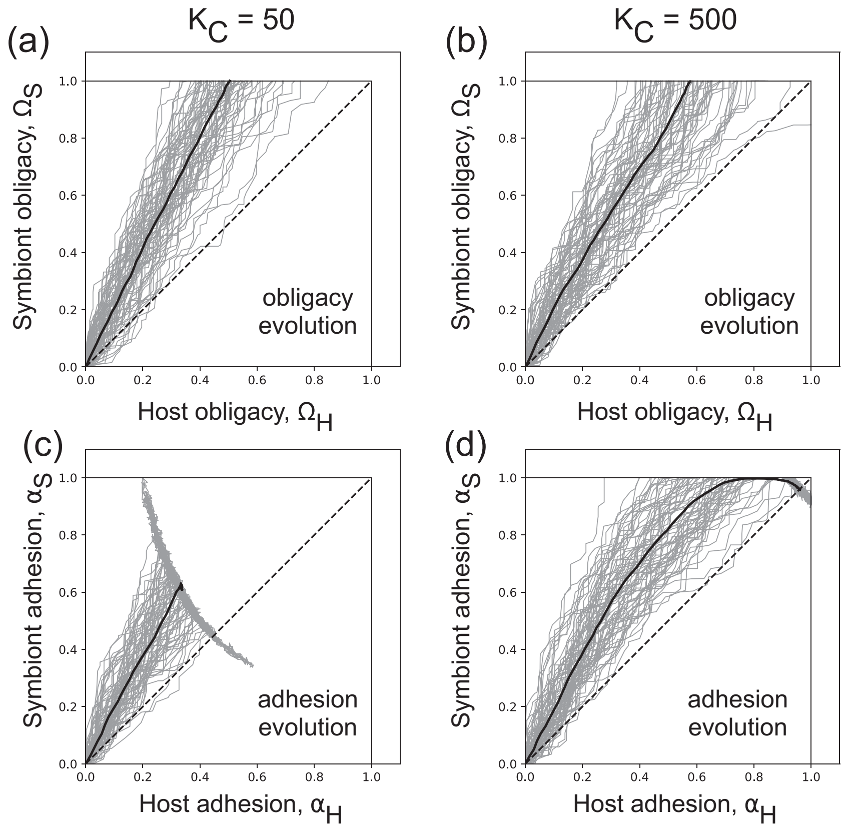

Figure 4: Collective carrying capacity qualitatively and quantitatively affects ultimate trait values. Each panel contains the results of 75 independent simulation runs (in gray), with the average trajectory in solid black. Both values of $K_C = 50$ and 500 in this figure are high enough to allow traits to increase from $(0, 0)$. $K_C = 10$ was not. When K_C is high enough, obligacies increase such that symbiont obligacy evolves to 1 and host obligacy subsequently is no longer under selection. Ultimate values of adhesion are affected by the precise values of K_C. The question of how high K_C must be is addressed in the main text. This outcome did not change between simulations run under low and high values of $r_C = 1$ and $r_C = 40$, respectively. Parameter values: $a_0 = 0.1$, $d = 50$, $r_H = 8$, $r_S = 20$, $r_C = 40$, $K_H = 100$, $K_S = 200$; K_C varies as indicated in the figure.

two values of the parameters K_C, both of which are high enough to allow traits to increase from $(0, 0)$ but are quantitatively different.

Obligacy evolution is not affected by the value of K_C. This is in line with our intuition developed in the previous sections—the defining event in an increasing obligacy trajectory is the location of its arrival at the unit square's boundary, and this cannot be affected by K_C, a parameter that does not bias trajectories preferentially toward hosts or symbionts. The bias $\Omega_S > \Omega_H$ does indeed persist, induced by the difference in host and symbiont population growth parameters—something we did not manipulate for these tests.

Adhesion trajectories, however, are affected by the precise value of K_C. This is because the important event here is the trajectory's arrival at the neutral ridge of ESSs described in the previous section. The presence of this ridge is explained by the nonmonotonically varying benefit that dissociation of collectives provides to independent host and symbiont populations. Therefore, it is intuitive that the ridge's location is affected by K_C, a parameter that strongly sets the equilibrium abundance of collectives. At lower K_C, the relative number of collectives is lower; hence, dissociation becomes nonbeneficial at relatively lower values of the adhesions and relatively higher values of the effective dissociation rate $d_0(1 - \alpha_H \alpha_S)$.

Note that the ridge when $K_C = 50$ also prevents the adhesions from reaching maximum values even for the symbiont (despite the bias $\alpha_S > \alpha_H$ persisting for identical reasons as above). When the carrying capacity K_C is very high (see the supplemental PDF, sec. S3.3), this ridge is extremely close to $(1, 1)$, and the adhesions effectively reach their maximum values. The slight movements around $\Omega_H(t^*_{\Omega_S})$ and the drift of adhesions along the ridge are artifacts of floating-point errors as before and can be ignored; we refrain from finding an involved artificial way to remove these, since their origin is provably clear (see previous sections).

The $r - K$ difference in importance is also reflected in the variation of the equilibrium population sizes as traits evolve (supplemental PDF, sec. S2.1). The pattern of variation supports the claims we have made so far—it is not qualitatively affected by the value of r_C but is so affected by changes in K_C. The ridge in population sizes can also be shown to be closer to $(1, 1)$ for higher K_C. This agrees with the intuition that the scale of the equilibrium population size x_C^* is set more strongly by K_C, with a smaller spread around it that is determined by other parameters. The maximum population size attained by the collective is its carrying capacity, and this takes place when at least one of $(\Omega_H, \Omega_S) = 1$ and when both $\alpha_H = \alpha_S = 1$.

Our analysis suggests that the pattern of variation switches depending on which quantity is bigger—dK_C or aK_HK_S (i.e., outflow or inflow into the population i when $\Omega_i = 1$). In particular, when $\Omega_H = \Omega_S = 0$, population sizes equilibrate to $x_H^* = K_H$, $x_S^* = K_S$; when $\Omega_i = 1$ for $i = \{H, S\}$, then $x_i^* = dK_C/aK_j$, where j is the other species. This suggests a sufficient condition on how high K_C must be: if $K_C > aK_HK_S/d$, hosts and symbiont populations are incentivized to increase obligacy. We tested this by varying a and d to perturb the same threshold quantity, and the results support our claim (see the supplemental PDF, sec. S3.2). These arguments are difficult to make fully explicit given intractable analytical results—a problem that we directly address in the next section.

Does Mutual Dependence Evolve Before or After Reproductive Cohesion?

To understand the coevolution of both obligacies and adhesions across the host and symbiont, we introduce a simpler version of model (1). The motivation is twofold: first, it allows for analytical tractability, enabling better understanding of our model; second, it restricts focus to the early evolutionary dynamics, since the dynamics at the boundaries is strongly dependent on the parameters b_i and d_i.

This simpler model assumes that the collective population exhibits unbounded exponential growth—that is, that the carrying capacity is infinitely high. The "exponential model" will henceforth refer to the following system of ordinary differential equations:

$$\begin{aligned} \dot{x}_H &= f_H x_H\left(1 - \frac{x_H}{K_H}\right) - a x_H x_S + d x_C, \\ \dot{x}_S &= f_S x_S\left(1 - \frac{x_S}{K_S}\right) - a x_H x_S + d x_C, \\ \dot{x}_C &= f_C x_C + a x_H x_S - d x_C. \end{aligned} \tag{8}$$

Analogously, system of equations (1) will now be referred to as the "logistic model" when necessary. One must keep in mind that comparisons to the logistic model of the previous sections can be made only when the traits Ω_i and α_i (and hence f_C; see mapping [2]) are of small value, since once f_C is high enough, the self-limitation term $-f_C x_C/K_C$ of the logistic growth rate becomes relevant. The formation of the collective can here be formally shown to be comparable to a mutualism between the host and symbiont (see the supplemental PDF, sec. S1.2).

Many statements can now be made regarding the existence, feasibility, and stability of population dynamical equilibria. The precise statements are relegated to the supplemental PDF (secs. S2.2, S4.2); however, the important features are that there is only one stable internal fixed point, which is feasible when the dissociation rate d is high enough to counteract the exponential growth of the collective. This is also borne out in the evolutionary dynamics of Ω_i and α_i under the exponential model (see the supplemental PDF, sec. S4.2); the traits increase until a point, and much before either has reached its maximum value, the collective's reproduction is so strong that no ecological equilibrium exists and the collective population blows up to infinity. Analogous to equation (5), an R_0 value can also be calculated here, and it is very close in functional form to the R_0 under the logistic model. In particular, it is given by

$$R_{0,\exp}(\tilde{\Omega}_H, \Omega_H, \Omega_S) = \frac{\tilde{f}_H + \dfrac{d a x_S^*}{(d - \tilde{f}_C)}}{\tilde{f}_H \dfrac{x_H^*}{K_H} + a x_S^*} \tag{9}$$

and is exactly the result of taking $K_C \to \infty$ in the logistic R_0 (see eq. [5]). This shows that the evolutionary dynamics captured by the exponential model are, at early trait values, truly comparable to logistic model (1). In fact, one can go further here and derive an exact invasion criterion—suppose a host mutant arises with obligacy $\tilde{\Omega}_H$ and adhesion $\tilde{\alpha}_H$. We show (supplemental PDF, sec. S4.2) that this mutant will invade if and only if

$$\frac{\tilde{f}_H}{\tilde{a}}\left(1 - \frac{\tilde{d}}{\tilde{f}_C}\right) > \frac{f_H}{a}\left(1 - \frac{d}{f_C}\right), \tag{10}$$

where quantities with a tilde are associated with the mutant. Since the host and symbiont are in our model identical in everything but the label we impose on them, an analogous criterion exists for the fate of a symbiont mutant. This criterion is "separable" into two quantities of the same functional form, each depending only on either the mutant or the resident. This implies that over the course of successive mutations, this underlying quantity

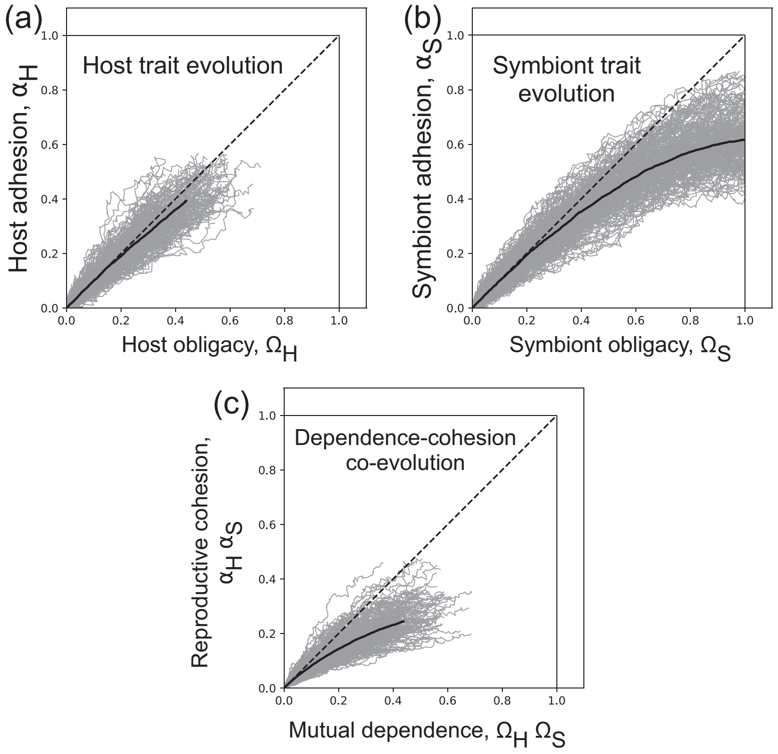

Figure 5: Mutual dependence evolves before collective reproduction. Here we consider the coevolution of the four traits Ω_H, α_H, Ω_S, and α_S under the exponential model (eqq. [8]). *a*, *b*, Both host and symbiont traits evolve such that, on average, $\Omega_i > \alpha_i$. Notice that symbiont evolution (*b*) shows that symbiont traits evolve to much higher values than host traits. *c*, Given the individual evolutionary trajectories of the host and symbiont, one can collate information to obtain measures that describe the collective as a whole—the degree of mutual dependence is represented here by the product $\Omega_H\Omega_S$ and the degree of reproductive cohesion by $\alpha_H\alpha_S$. We observe that mutual dependence evolves faster than reproductive cohesion. The trajectories stop when they hit the feasibility bound; it is nontrivial to visualize its manifestation in this plane and is hence absent. Parameter values: $K_H = 100$, $K_S = 200$, $K_C = 500$, $a_0 = 0.1$, $r_H = 8$, $r_S = 20$, $r_C = 10$, $d_0 = 50.0$.

is maximized. The existence of such an optimization principle (Gyllenberg and Service 2010) also means that there can never be evolutionary branching in our traits at these early times (see the supplemental PDF, sec. S4.4). Finally, using the constraints we set up in “An Eco-Evolutionary Model” and section S1.1 of the supplemental PDF, it can also be shown that all four traits Ω_H, Ω_S, α_H, and α_S must monotonically increase over evolutionary time.

To study dependence-cohesion coevolution, we again consider the mapping in equations (2); results of the simulations are shown in figure 5. We represent the degree of dependence between the host and symbiont by the product $\Omega_H\Omega_S$ of their obligacies and the degree of reproductive cohesion by $\alpha_H\alpha_S$.[1]

These results show two important facts. First, for both the host and the symbiont, it is adaptive to evolve such that $\Omega_i > \alpha_i$; that is, obligacy increases faster than adhesion. Focusing on $\Omega_H\Omega_S$ and $\alpha_H\alpha_S$, one concludes that evolutionary trajectories are biased toward more mutual dependence than reproductive cohesion. This is a central result. It shows that, over time, we expect that a host-symbiont collective evolves such that the partners are closer to complete mutual dependence than to reproducing synchronously.

Fundamentally, this is because the functional effects of the pairs of traits are different. Recall that both trait pairs increase because of the better growth of the collective. However, there is a difference between them: independent growth of type i ($i \in \{H, S\}$) is a function only of Ω_i, whereas the effect of the α_i occurs only in “coordination” with both species, since dissociation is a function of the product of α_H and α_S (see eqq. [2]). Therefore, an increase in Ω_i has a higher functional effect (in increasing the invasion fitness) than the same increase in α_i, since the latter's effect is damped by the other adhesion as well (since $\alpha_i \in [0, 1]$). See section S4.5 of the

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[1] The multiplicative form here is connected to how they map to ecological parameters—a multiplicative effect of the Ω_i on collective reproduction f_C motivates the interpretation of $\Omega_H\Omega_S$ as the degree of mutual dependence as opposed to other potential measures, such as $\Omega_H + \Omega_S$.

supplemental PDF for a more comprehensive explanation via other functional form choices.

This result is robust to the choice of parameter values, different generation times, additive (instead of multiplicative) effect of the individual traits on the collective, and so on (fig. S14). The bias persists, and mutual dependence evolves faster than reproductive cohesion. This strongly suggests that endosymbioses in nature are more likely to be mutually dependent than cohesive.

Conclusions and Conjectures

Endosymbiosis and the advances in complexity it made possible are astonishing. An endosymbiotic association led to eukaryotes and many other intricate associations between unrelated individuals. In this study, we endeavour to give a precise view of endosymbiosis as an egalitarian evolutionary transition in individuality and study the effect of some essential ecological factors on its origins.

We study two significant characteristics of an endosymbiotic collective undergoing an evolutionary transition—the reproductive cohesion of the host and symbiont (affected by host and symbiont adhesion, α_H and α_S) and the level of mutual dependence between them (obligacy, Ω_H and Ω_S). Our model shows that when obligacies evolve independently, one expects the symbiont obligacy to increase to its maximum value first, which can lead to the host obligacy being under selection to increase, decrease, or stay constant under different ecological scenarios. This might explain the diversity in dependence outcomes that we see in nature, and we identify the two parameters in our model, b_i and d_i $(i = H, S)$, that control this outcome. The adhesions also increase (with symbiont adhesion reaching high values first), ultimately leading to the accumulation of neutral variation due to drift of the evolutionary trajectory along a line of ESSs. The final value of the adhesions depends on the collective carrying capacity. Second, we show that host-symbiont asymmetries in evolutionary outcomes arise because of differences in their population growth rates and carrying capacities. Last, we show that at early evolutionary times, the density of permitted evolutionary trajectories in the dependence-cohesion plane is not uniform: when Ω_i and α_i coevolve, both species evolve to be more obligate than adhesive, irrespective of the rate of these traits' evolution.

Our work highlights the importance of considering differences between host and symbiont population growth parameters. That the symbiont trait (either obligacy or adhesion) increases faster than its host counterpart is due to the symbiont's larger population size and hence faster rate of evolution: an instantiation of the Red King effect (Bergstrom and Lachmann 2003; Frean and Abraham 2004). Such a bias must be expected when host and symbiont interests are aligned, and defection (lower Ω or α) leads to a lower payoff. In the original Red King effect, the interest-aligning mechanism is a mutualism—an ecological interaction. Our analysis shows that the collective's formation (and shared fate) is another fundamental interest-aligning mechanism in evolutionary transitions. Furthermore, this faster rate of evolution has qualitatively novel effects in our model: in the case of obligacy, the symbiont evolves to full obligacy first, which leads to conditions where the host obligacy can be under selection to increase, decrease, or neutrally drift. Our model predicts full dependence for the interaction partner with higher growth rate and carrying capacity and parameter-dependent scenarios for the partner with lower growth rate and carrying capacity. There are at least two more qualitatively different routes to asymmetric investments. First, the growth tradeoffs $f_H(\Omega_H)$ and $f_S(\Omega_S)$ for host and symbiont investing in collective reproduction might be different and might in nature take nonlinear forms. The work of Estrela et al. (2015) suggests that this might have a qualitative impact: in their model, obligate exploitation can be observed over mutual dependence when the growth benefit of losing a costly function is accelerating in the amount of function lost. Furthermore, we assumed that the within-collective reproduction and mortality rates are identical for host and symbiont. We assumed this for explanatory clarity, but it is almost certainly not true and will give rise to new layers of asymmetry. Since these parameters are central to the evolutionary outcome, it is imperative in future work to measure them experimentally and characterize differences in their values. Developing this part of the theory might also help understand why current host-symbiont relationships are often biased toward the symbiont being much more obligate than the host. This is clearest in the evolution of tiny genomes in endosymbionts (McCutcheon and Moran 2011; Moran and Bennett 2014; Bennett and Moran 2015), and the ability to go through symbiont loss and replacements in some hosts (Chong and Moran 2018). However, reductive genome evolution has also been shown to be driven by other mechanisms, such as Muller's ratchet (Moran 1996) or environment-induced redundancy (McCutcheon and Moran 2010; Morris et al. 2012; Husnik et al. 2013), in addition to Red King–type effects. These latter effects are predicated on endosymbionts occurring within the hosts and not the other way around. Simple factors such as growth parameters and the nested structure of endosymbioses are therefore clearly important, and further work is required to delineate their consequences from that of complicated strategies, such as partner choice/sanction or zero-determinant strategies (Press and Dyson 2012; Daubech et al. 2017).

Another main aim was to understand why an evolutionary transition does not always take place. In this context, our model suggests the importance of the within-collective birth and death rates. They control model behavior at two important time points: whether the obligacies initially increase, and what happens to the host obligacy once the symbiont becomes completely obligate. If within-collective births are stronger than deaths, (i) both obligacies increase initially and (ii) host obligacy decreases to zero once the symbiont has become obligate. If the opposite is true (i.e., within-collective deaths are stronger than births), (i) the obligacies increase only above a certain threshold initial value and (ii) the host becomes completely obligate once the symbiont has done so. Our model thus demonstrates that the evolutionary dynamics of dependence can impose strong constraints on the emergence of obligate endosymbioses. If the within-collective rates depend on the evolving traits Ω_i and α_i, it would allow for the situation where births are stronger than deaths initially (so both host and symbiont obligacies initially increase) and deaths are stronger than births later (and hence both become fully obligate). However, the rates may depend on different (combinations of) traits, and different dependence structures of b_i, d_i on Ω_i, α_i $(i \in \{H, S\})$ might have different consequences. The values of b_i and d_i also need not be equal in the way that we have considered. Understanding the consequences of these extensions constitutes, in our view, the next study necessary in this body of work. Last, full adhesions can be achieved only when the collective carrying capacity is very high; when it is lower, final adhesion values must be interpreted carefully, since our model predicts drift over time and hence variability.

The prediction that dependence evolves faster than cohesion at early times can also be confronted with biological examples. Following the work of Estrela et al. (2016), we compiled a short, nonexhaustive list of well-studied endosymbioses (table 3) where there is information on the level of vertical transmission (a proxy for reproductive cohesion) and the degree of mutual dependence. However, because of the qualitative nature of the data, the causal mechanics of the interactions are inconclusive. Some cases show direct connection to our theory (in the *Riftia-Endoriftia* endosymbiosis, there is high dependence but with horizontal transmission), others do not (the *Dictyostelium-Burkholderia* farming symbiosis is facultative from both sides and has a mixed mode of transmission; DiSalvo et al. 2015). It is impossible to compare the degree of dependence and cohesion here. There is indirect evidence that mutual dependence is easier to evolve than reproductive cohesion, since it is widely observed empirically (Kost et al. 2023); is understood well, via, for example, the Black Queen effect (Morris et al. 2012); can evolve rapidly in an experiment (D'Souza and Kost 2016); and in principle requires very few traits (Estrela et al. 2015). On the other hand,

Table 3: Dependence and cohesion information in some well-studied symbioses

Host-symbiont	Degree of dependence	Mode of transmission	Reference(s)
Ancestral eukaryote host–protomitochondra, protoplastid	Mutually obligate	Vertical	Sagan 1967
Aphid–*Buchnera aphidicola*	Mutually obligate	Vertical	Buchner 1965; Gündüz and Douglas 2008; Vogel and Moran 2010; Hansen and Moran 2011
Riftia-Endoriftia	Host obligate, symbiont facultative	Horizontal	Felbeck and Jarchow 1998; Nussbaumer et al. 2006
Dictyostelium discoideum–Burkholderia	Both facultative	Mixed	DiSalvo et al. 2015
Squid-*Vibrio* (not intracellular)	Both facultative	Horizontal	McFall-Ngai 2014
Pea aphid–*Regiella*	Both facultative	Vertical, horizontal possible	Scarborough et al. 2005; Gehrer and Vorburger 2012
Legume-rhizobium	Both facultative	Horizontal	Kiers et al. 2003; Denison and Kiers 2011
Flatworm-*Riegeria*	Host obligate, symbiont dependence unclear	Vertical	Gruber-Vodicka et al. 2011
Rhopalodia–nitrogen-fixing *Cyanobacteria*	Mutually obligate	Vertical	Prechtl et al. 2004
Cicada–*C. sulcinia*/*hodgkinia*	Mutually obligate	Vertical	McCutcheon et al. 2009

Note: This table is a survey of symbioses for which there is nontrivial information on the degree of dependence and the mode of symbiont transmission (a proxy for reproductive cohesion), adapted from a similar table compiled by Estrela et al. (2016). The information present, however, is (i) qualitative and (ii) a snapshot of the current state. The current state does not carry information about the full evolutionary trajectory and hence is insufficient to estimate the traits Ω_i and α_i. Therefore, the available information does not allow us to confirm or refute the bias toward mutual dependence our work predicts.

few studies have precisely estimated quantities related to the level of vertical and horizontal transmission (Darby and Douglas 2003; Hosokawa et al. 2007). Furthermore, it is not clear whether there are genetic constraints that would lead to correlations in obligacy and adhesion—a strong enough correlation could shift in a new direction the bias toward codependence we observe. On the theoretical side, an interesting extension of our model is to understand whether the bias toward dependence we see survives to later evolutionary times, when traits are closer to their final values. This study and its limitations thus highlight the need for a tighter connection between empirical work and theory and the requisite experiment where the complete evolutionary transition can be quantified.

Nonetheless, taken as a null model, our study shows that an evolutionary transition in individuality is far from an inevitable outcome of the existence of a higher level of selection, suggesting that one might need to invoke different mechanisms to explain phenomena such as eukaryogenesis. While our model already allows for many of the scenarios that one would like to capture, many possible extensions exist that could improve the biological realism. Perhaps most importantly, we consider here the extreme case of the interaction becoming beneficial only in close proximity; one can also construct a model where interaction benefits are relevant even outside the collective. This would add Lotka-Volterra-type cross terms to the ecological dynamics captured by the system of equations (1). Additionally, we set the collective's carrying capacity K_C to a constant value independent of host or symbiont traits, since we envision that the mechanism of benefit exchange underlying this endosymbiosis enables the colonization of a new niche (broadly construed) and that this niche has an associated carrying capacity. Better or worse usage of the niche (via different trait values) does not guarantee a higher maximum occupancy, only a quicker rate of reaching it. Furthermore, we consider that the collectives must always be formed by a fixed density of symbionts acquired together and only once—that is, we do not consider symbiont growth inside a single host. The size of these symbiont blocks does not affect the dynamics of our model per se, so one can think of a single symbiont inside each host without loss of generality. However, in reality each host has a dynamically changing symbiont population, and successive symbiont acquisition events would allow, for example, decreasing symbiont population sizes to be propped up by immigration or to be qualitatively changed by mutualism or antagonism between different symbiont strains (see Patel and West 2022). Selection on the host due to the interactions with multiple symbionts might add further selection pressures that lead to a transition. Last, we also do not consider that there might be competition between the independent types and the collective due to niche overlap. Relaxing each of these assumptions is a worthy and important direction for future work.

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Statement of Authorship

Conceptualization: C.S.G., P.C., G.S.A.; funding acquisition: C.S.G.; model development and analysis: G.S.A., P.C., C.S.G.; computer scripts: G.S.A.; supervision: C.S.G.; writing—original draft: G.S.A.; writing—review and editing: P.C., C.S.G., G.S.A.

Data and Code Availability

All data and simulation code for generating the figures are available on Zenodo (https://doi.org/10.5281/zenodo.14685762; Athreya et al. 2025).

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