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Symbiosis Without Mutualism and the Merger of Lineages in Evolution

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IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 22

The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

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The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

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Contents

Abstract

A model for the coevolution of two species in facultative symbiosis is used to investigate conditions under which species merge to form a single reproductive unit. Two traits evolve in each species, the first affecting loss of resources from an individual to its partner, and the second affecting vertical transmission of the symbiosis from one generation to the next. Initial conditions are set so that the symbiosis is not mutualistic and vertical transmission is very rare. It is shown that a stable symbiotic unit with maximum vertical transmission of the partners can evolve in the face of continued exploitation of one partner by the other. Such evolution requires that eventually deaths should exceed births for both species in the free-living state, a condition which can be met if the victim, in the course of developing its defences, builds up sufficiently large costs in the free-living state. This result expands the set of initial conditions from which separate lineages can be expected to merge into symbiotic units, and argues against any automatic assumption of mutualism between organisms with a long history of symbiosis.

Keywords: Adaptive dynamics, Coevolution, Major transitions in evolution, Mutualism, Symbiosis, Vertical transmission

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Symbiosis Without Mutualism and the Merger of Lineages in Evolution

Richard Law
Ulf Dieckman

1. Introduction

Evolutionary biologists are accustomed to think of macroevolution as a branching process in which lineages diverge as they descend from common ancestors, giving rise to a tree-like phylogeny (Darwin 1859: 56). This picture is reinforced in many studies, a good example being the phylogeny of life based on comparisons of the small subunit of ribosomal RNA (Sogin 1991).

While in no way questioning the central role of this mode of evolution, here we consider the reverse process in which lineages, remote by descent, merge to form symbioses capable of reproducing themselves as a single unit. (In using the term 'symbiosis', we do not mean to imply a mutualistic association; we simply mean that the association is potentially longlasting (Lewis 1985).) There is no doubt that such mergers have happened, a striking example being the evolution of the chloroplast of eukaryotes. This is thought to have begun with one or more mergers of photosynthetic gram-negative bacteria and early eukaryotes arguably about 2 Bya (Dyer & Obar 1994:12). Following this, there seems to have been a complex sequence of changes perhaps involving the transfer of chloroplasts of one eukaryote to another (euglenoids and dinoflagellates), and uptake of complete photosynthetic eukaryotes by other eukaryotes (cryptomonads, diatoms and brown algae) (Cavalier Smith 1992; MacFadden & Gilson 1995).

The emergence of new, symbiotic units built from independent subunits lies at the heart of some of the major steps in the evolution of life (Buss 1987; Maynard Smith & Szathmáry 1995). How the transition is achieved is not at all obvious, since it is quite possible for natural selection, operating at the level of the subunits, to disrupt their integration into the larger unit. It is particularly difficult to see how it can come about in cases where the subunits are genetically unrelated and there is no opportunity for kin selection to take place. Attempts to find evolutionary paths leading to integration of unrelated organisms have usually presupposed that each subunit can provide some benefit to its partner so that the success of one is bound to the success of the other; the hypercycle of prebiotic evolution is a case in point (Eigen & Schuster 1977). But evolution of cooperative associations can be difficult to get started as the benefit each species provides to its partner may have to be greater than a threshold value (Frank 1995).

Arguably a more likely starting point would involve the exploitation of one partner by the other. One way in which a symbiotic unit could emerge from such an initial state is through vertical transmission (Fine 1975); if the continued existence of the exploiter depends in part on its partner's survival, it will not pay to exploit the partner too heavily (Ewald 1987). Yamamura (1993, 1996) showed that an obligate parasite which starts with enough vertical transmission will cause evolution of greater vertical transmission and a decrease in exploitation, leading eventually to a mutualistic symbiosis.

This paper shows that a stable symbiotic unit with coupled reproduction of the partners can evolve from a facultative association in the face of continued exploitation of one partner by the other; mutualism is not a necessary feature of a stable symbiotic unit. What is needed for such a unit to emerge is that, in the free-living state of both partners, deaths should exceed births. This can be achieved through mutualism, but it can also be achieved through costs incurred by the victim as it evolves in association with the exploiter, as documented in a bacterial infection of *Amoeba proteus* (Jeon 1972). This result expands the set of initial conditions from which separate lineages can be expected to merge into symbiotic units (Frank 1997), and suggests that organisms with a long history of symbiosis should not be assumed, a priori, to be mutualistic.

2. A coevolutionary model of symbiosis

We investigate the interaction of two species, indexed 1, 2, utilizing separate resources in the free-living state. When the species come together, they can form a symbiosis, and there is transfer of resources between the partners. Species 1, the *exploiter*, restricts the flow to its partner more than the other, the *victim*. The composite, symbiotic unit may be temporary, or it may have a more extended existence; we emphasize its separate existence by calling it the *holobiont*, following Margulis (1993: 169).

To examine the evolution of the community, we use a dynamical system coupling two phenotypic traits in each species. The first affects the transfer of resources from the species to its partner; we refer to the value of this trait as s_{i1} for species i. The second affects the probability of coupled birth events of the partners in symbiosis. Such coupled births maintain the integrity of the holobiont from one generation to the next and are critical for merger of the lineages. We refer to the value of this second trait as s_{i2} for species i. The four trait values that predominate at a given time are collected into a vector $s = (s_{11}, s_{12}, s_{21}, s_{22})$.

How the traits evolve depends on the abundance and phenotypic state of each species and its partner, an environment which itself is evolving. Disentangling the causal pathways involved is not trivial, and it helps to think of a hierarchy of three separate time scales: a microscopic (physiological) scale on which resources are taken up by individuals, a mesocopic (ecological) scale on which the population dynamics determining abundance occur, and a macroscopic (evolutionary) scale on which phenotypic change takes place (Dieckmann & Law 1996; Marrow *et al*. 1996). Abundance of the species is then set by the current phenotypic states, but gradually changes as the system evolves.

Microscopic time scale. We start with the smallest, physiological, time scale, on which abundances and trait values can be taken as constant. To keep a simple mechanistic underpinning for the phenotypic traits and their effects on birth and death events, we use a resource-based model; Figure 1 shows the flows involved. We assume that there are two resources 1 and 2, at an external concentration C_1, C_2 in the environment; they might, for instance, be thought of as two sources of carbon. In the free-living state, species i utilizes resource type i only; in symbiosis, however, resource j

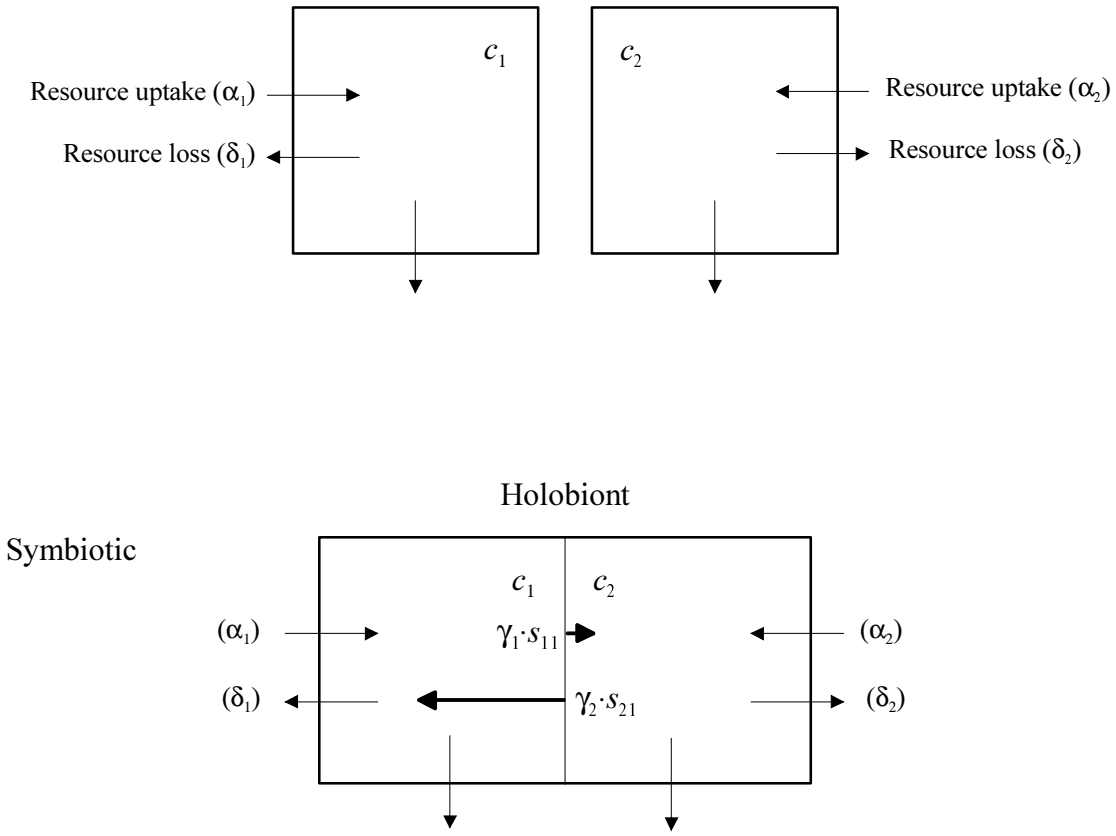

Figure 1. Model of resource dynamics across the boundaries of free-living and symbiotic individuals of two species. The heavy arrows refer to flow of resources between individuals in symbiosis, and there is net flow of resources from the victim to the exploiter. Internal concentrations of resource are c_1, c_2. Greek symbols are rate constants used in Appendix equation (A1).

can move into species *i*, in so doing being converted into resource *i*. The resource concentration within each individual comes rapidly to equilibrium, and the birth rate of the individual is proportional to this concentration. Details of resource flows in and out of individuals, and how these determine the per capita rates of reproduction, are given in the Appendix.

Mesoscopic time scale. We now turn to the time scale of ecological dynamics and define a system of equations for the dynamics of population size n_1, n_2, and $\tilde{n}$ of the exploiter, victim and holobiont respectively, still holding the trait values constant.

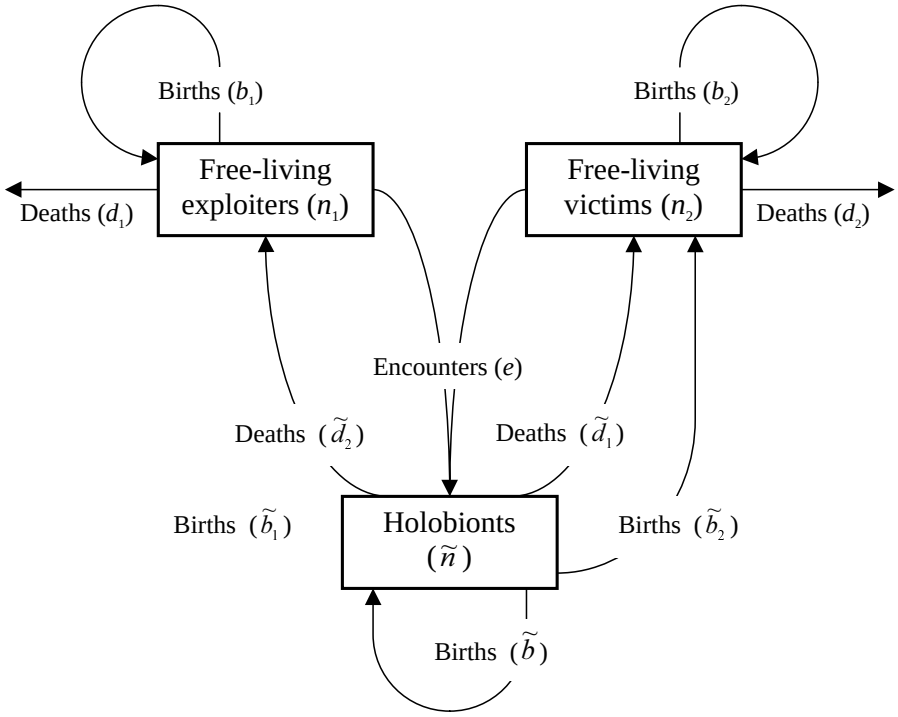

Figure 2. Model of population dynamics, showing the flows between populations of free-living exploiters, victims and holobionts, with population sizes n_1, n_2, $\tilde{n}$. Other symbols are rate constants used in equation (1).

The flows between these populations are shown diagrammatically in Figure 2, and the dynamics are given by

$$\dot{n}_1 = +b_1 \cdot n_1 - d_1 \cdot n_1 - e \cdot n_1 \cdot n_2 + \tilde{b}_1 \cdot \tilde{n} + \tilde{d}_2 \cdot \tilde{n} \quad (1a)$$

$$\dot{n}_2 = +b_2 \cdot n_2 - d_2 \cdot n_2 - e \cdot n_1 \cdot n_2 + \tilde{b}_2 \cdot \tilde{n} + \tilde{d}_1 \cdot \tilde{n} \quad (1b)$$

$$\dot{\tilde{n}} = -\tilde{d}_1 \cdot \tilde{n} - \tilde{d}_2 \cdot \tilde{n} + e \cdot n_1 \cdot n_2 + \tilde{b} \cdot \tilde{n} \quad . \quad (1c)$$

The tildas here and below identify terms that apply to the symbiotic state. These equations are perhaps the simplest formulation that makes explicit both the free-living and symbiotic states. They include the rate at which free-living individuals of species *i* give rise to free-living offspring (b_i), the rate at which symbiotic individuals of *i* give rise to free-living ($\tilde{b}_i$) and symbiotic ($\tilde{b}$) offspring, the death rates of species *i* in the free-living (d_i) and symbiotic ($\tilde{d}_i$) states, and encounters at rate *e* between free-living individuals creating holobionts.

The populations are regulated by the availablity of resources C_1, C_2 in the environment, as described in the Appendix. An effect of this is the existence of an equilibrium point at which both species have positive population sizes, which is the solution in all our integrations that start with positive populations. Thus, on the mesoscopic time scale, the populations tend to these equilibrium abundances for constant trait values. For interpretation of the conditions for increase of mutants used later, it should be noted that, once equilibrium has been reached, the following property applies to each species:

$$\tilde{d}_i < \tilde{b}_i + \tilde{b} \;\Leftrightarrow\; d_i > b_i \quad ; \tag{2}$$

in other words, if births exceed deaths in the symbiotic state, then deaths must exceed births in the free-living state.

Mutant trait values. Consider now a community which has reached equilibrium population sizes for a given vector s of resident trait values. To describe the evolutionary dynamics, we need to know whether a mutant trait s'_{ij} is able to spread, when it enters the community. These mutants affect the birth rates in symbiosis, and we write the birth rates at ecological equilibrium as functions $\hat{\tilde{b}}_i(s'_{ij}, s)$, $\hat{\tilde{b}}(s'_{ij}, s)$, the first argument being the mutant trait value of the individual itself, and the second being the trait values of the resident community in which it lives. In the free-living state, the birth rate $\hat{b}_i(s)$ is unaffected by mutation and has only one argument, the state of the resident community.

How the traits affect birth rates in symbiosis is shown schematically in Figure 3. The first trait s'_{i1} scales the rate at which the individual loses resource to its partner; this is a dimensionless quantity in the range [0, 1]. With the assumptions made above about resource flow between the symbionts, the total birth rate of a symbiotic individual $\hat{\tilde{B}}_i(s'_{i1}, s)$, defined by summing over both its free-living and symbiotic progeny, decreases linearly as the rate at which it loses resource to its partner increases; the individual therefore produces more offspring the smaller s'_{i1} is.

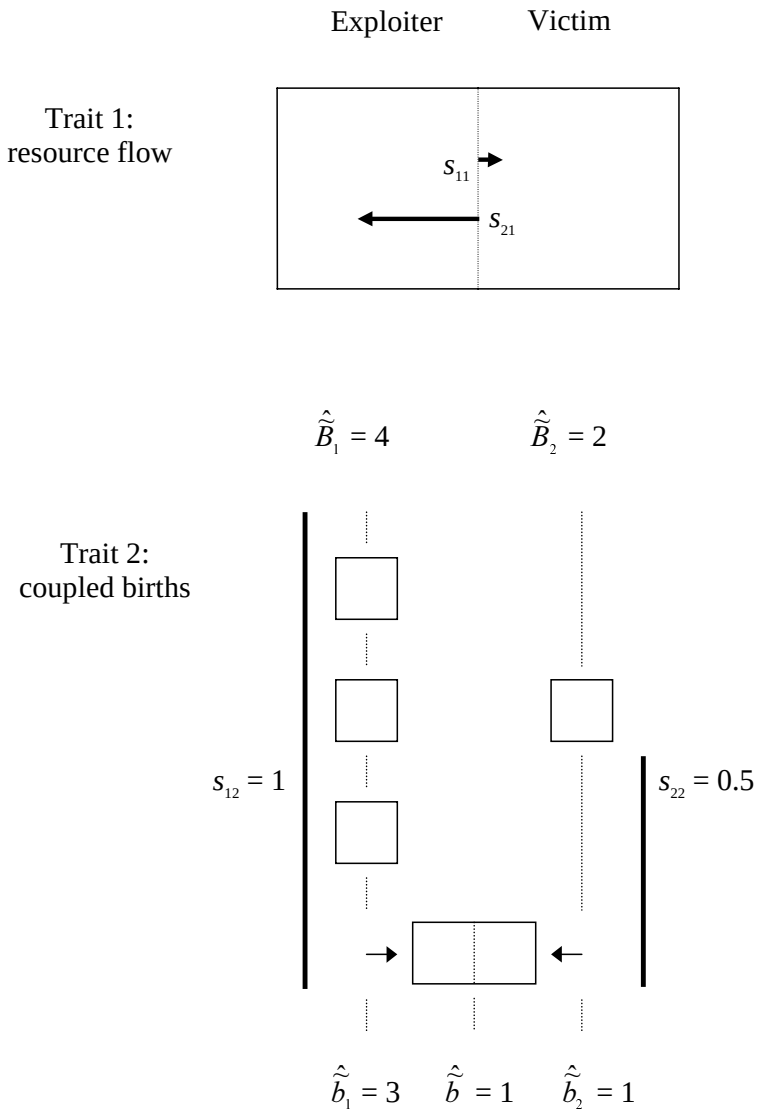

Figure 3. Model of adaptive dynamics, showing effects of traits s_{ij} on birth rates in symbiosis. The first trait, affecting how much resource is lost to the partner, gives the exploiter a greater birth rate. The second affects the proportion of births which are symbiotic; a numerical example is given showing how the total birth rate of symbionts is partitioned between symbiotic and free-living offspring.

The second trait s'_{i2} affects the probability of a coupled birth event in symbiosis; this is also dimensionless in the range [0,1]. This trait partitions the total birth rate of symbiotic individuals among free-living and symbiotic offspring. We make the assumption that the rate at which symbiotic offspring are born depends on the product $s_{12} \cdot s_{22}$ over both species; it is then enough for one species to have a trait value $s_{i2} = 0$ for there to be no coupled births. The rate at which these holobiont births occur is taken

to be $\hat{\tilde{b}}(s'_{i2}, s) = \min\left(\hat{\tilde{B}}_i(s'_{i2}, s) \cdot s'_{i2} \cdot s_{k2}\ ,\ \hat{\tilde{B}}_k(s_{k2}, s) \cdot s'_{i2} \cdot s_{k2}\right)$ where $k \neq i$. So the rate at which symbiotic offspring are born is the same for both species (there is one individual of each species in the offspring), and we adjust the rate at which free-living offspring are born accordingly: $\hat{\tilde{b}}_i(s'_{i2}, s) = \hat{\tilde{B}}_i(s'_{i2}, s) - \hat{\tilde{b}}(s'_{i2}, s)$. A numerical illustration of how this works is given in Figure 3.

A cost to evolution will also be considered below. We introduce this as a death-rate $\hat{d}_i(s'_{i1})$ in the free-living state which increases as s'_{i1} diverges from the value $s_{i1}^{(0)}$ before evolution starts. This is motivated by results of Jeon's (1972) study of a bacterial infection of *Amoeba*, a rare instance of an experimental study of evolution of symbiosis. From an initial state in which *Amoeba* colonies were able to grow much faster in the absence of the bacteria than in their presence, the *Amoeba* evolved to a state of low viability when deprived of the bacteria. We use a function symmetric around $s_{i1}^{(0)}$ to describe such a cost:

$$d_i(s'_{i1}) = D_i \cdot \exp\left(\omega_i \cdot (s'_{i1} - s_{i1}^{(0)})^2\right) \tag{3}$$

where D_i is the free-living mortality rate before evolution starts, and ω_i is a constant scaling how fast the cost grows.

Macroscopic time scale. We now turn to a longer, evolutionary, time scale on which mutations occur and replace resident traits. In making this separation of time scales, we are assuming that mutations are sufficiently rare for the populations to get close to their equilibrium sizes between mutation events.

At a qualitative level, quite a lot about phenotypic evolution of a symbiotic system can be learnt simply from the sign of the average initial rate of increase of a mutant (Kato & Yamamura 1997). Specifically, writing $N'_i = (n'_i, \tilde{n}')$ as the size of the mutant population, the average rate $\dot{N}'_i$ at which it grows when rare is given by

$$\dot{N}'_i = N'_i \cdot L_i \quad , \tag{4a}$$

where

$$L_i = \begin{pmatrix} \hat{b}_i(s) - d_i(s'_{i1}) - e \cdot \hat{n}_k(s) & e \cdot \hat{n}_k(s) \\ \hat{\tilde{b}}_i(s'_{ij}, s) + \tilde{d}_k & \hat{\tilde{b}}(s'_{ij}, s) - \tilde{d}_i - \tilde{d}_k \end{pmatrix} , \tag{4b}$$

and $k \neq i$. The resident community can be taken as remaining at the equilibrium abundances $\hat{n}_1(s), \hat{n}_2(s), \hat{\tilde{n}}(s)$, set by the resident trait values, when the mutant is rare. For a mutation of small enough effect on the phenotype, the average initial rate of increase λ of the mutant (i.e. the dominant eigenvalue of L_i), which must be positive for the mutant to stand any chance of becoming established, is given to a good approximation by the determinant and trace of L_i (Kato & Yamamura 1997):

$$\lambda = \det L_i / \mathrm{tr}\, L_i > 0 \quad . \tag{5}$$

Generically, this approximation for the eigenvalue becomes exact for $s'_{ij} \to s_{ij}$. With this expression it is possible to find relatively simple conditions for the spread of mutants.

To describe the evolutionary dynamics in quantitative terms, we work from a stochastic mutation-selection process. The first source of stochasticity is mutation itself; a mutant birth, with trait value s'_{ij}, is drawn at random from a mutation distribution $M_{ij}(s'_{ij} - s_{ij})$ symmetric around the current resident trait value s_{ij} and with small variance. The second source is the chance of extinction of the mutant when rare; since the mutant begins existence as a single individual, it may be lost through demographic stochasticity irrespective of how advantageous it is (Fisher 1958: 80 *et seq.*; Dieckmann & Law 1996). A mutant which escapes extinction when rare is assumed to go to fixation. Evolution of the traits can be approximated by the mean path of the stochastic process, using a system of four equations (A8) derived in the Appendix. These equations describe the coupled, adaptive dynamics of the four traits. As each trait evolves, it changes the environment in which the species live, and this affects the future path of evolution of each trait; each species both constructs and is changed by its environment (Lewontin 1983; Odling-Smee *et al*. 1996).

3. Results

We can now determine conditions needed for development of a holobiont which, by means of coupled births, maintains its integrity as a symbiotic unit from one generation to the next. Below, two cases are considered: (1) evolution with no costs, in which the rate of coupled births does not increase substantially, and (2) evolution with costs, where it can become advantageous to both partners to remain in symbiosis from one generation to the next.

In describing these cases, we assume that the following starting conditions apply. (1) Mixing between the free-living and symbiotic states is large enough for $\mathrm{tr}\, L_i < 0$; our numerical studies indicate that this is readily satisfied, and this means that a mutant can spread if and only if $\det L_i < 0$ (see inequality (5)). (2) Traits affecting resource flow begin with the property $s_{11} = 0, s_{21} > 0$; species 1 is then the exploiter and species 2 the victim. (3) Traits affecting coupled births (s_{12}, s_{22}) start close to zero; this means that it is very rare for continuity of the symbiosis to be maintained from one generation to the next. Throughout it is assumed that mutants cause no more than small effects on the phenotype.

Cost-free evolution. Consider a mutant s'_{i1} in species *i* that reduces the loss of resource to its partner in symbiosis, thereby gaining a small increment $\delta\hat{\hat{b}}_i + \delta\hat{\hat{b}}$ to its birth rate in symbiosis. In the absence of any cost, the death rate of individuals in the free-living state is constant, $d_i(s'_{i1}) = D_i$, and, from inequality (5), the mutant can only increase if

$$0 \;<\; \underbrace{\left(D_i - \hat{b}_i(s)\right)\cdot\delta\hat{\hat{b}}}_{I} \;+\; \underbrace{e\cdot\hat{n}_k(s)\cdot\left(\delta\hat{\hat{b}}_i + \delta\hat{\hat{b}}\right)}_{II}\;, \qquad (6)$$

where $k \neq i$. This condition is satisfied for the exploiter: it has an excess of births over deaths in symbiosis, and correspondingly an excess of deaths over births in the free-living state (inequalities (2)), so term *I* is positive; term *II*, comprising only positive factors, is also positive. Thus s_{11} is held at zero by natural selection as the symbiosis evolves. In the case of the victim, our numerical results indicate that, due to the strong mixing, term *II* is large enough for the condition to be met for this species as well. This

is just as one would expect: a mutant which reduces the loss of resources to its partner, has a birth rate in symbiosis greater than that of the resident phenotype, irrespective of how these births are partitioned among free-living and symbiotic offspring. Evolution continues until the species have erected a complete barrier to resource movement in symbiosis, at which point the birth rates in symbiosis are the same as they are free-living, and the symbiosis is neutral.

Consider now a mutant s'_{i2} in species *i* that redistributes births by symbiotic parents among free-living and symbiotic states, making a small increment $\delta\hat{\hat{b}}$ to the coupled births, and correspondingly a small reduction $-\delta\hat{\hat{b}}$ to free-living births.

On the average, such a mutant will increase if

$$0 < \left(D_i - \hat{b}_i(s)\right) \cdot \delta\hat{\hat{b}} \qquad . \tag{7}$$

What matters here is that deaths should exceed births in the free-living state. This is certainly the case for the exploiter; it has more births than deaths in symbiosis, and correspondingly more deaths than births when free-living [inequalities (2)]; mutants with $s'_{12} > s_{12}$ are therefore favoured. But the reverse applies to the victim, and this selects mutants $s'_{22} < s_{22}$. The resulting conflict prevents a concerted shift towards more coupled births needed for the holobiont to maintain its integrity from one generation to the next. Eventually the symbiosis reaches a state in which the barriers to resource flow in symbiosis are complete ($s_{11} = s_{21} = 0$) at which point there is no further selection on coupled births at all.

An illustration of this evolution, obtained by integration of equations (A8), is shown in Figure 4a. This indicates the downward path of s_{21}; s_{11}, which starts at zero, is held at zero by selection. How the rate of coupled births changes depends quantitatively on the rate at which s_{12} increases and s_{22} decreases. But there is little change in this before s_{21}, like s_{11}, is zero, and s_{12} and s_{22} have become neutral.

Evolution with costs. The evolutionary path above would end matters, were it not for costs associated with defence. But the outcome can be quite different if, as in the case of Jeon's (1972) *Amoeba*, there is some loss of viability in the free-living state as the victim evolves in response to its symbiotic partner. To see the effect of this, we repeat the analysis above with a cost as given in equation (3).

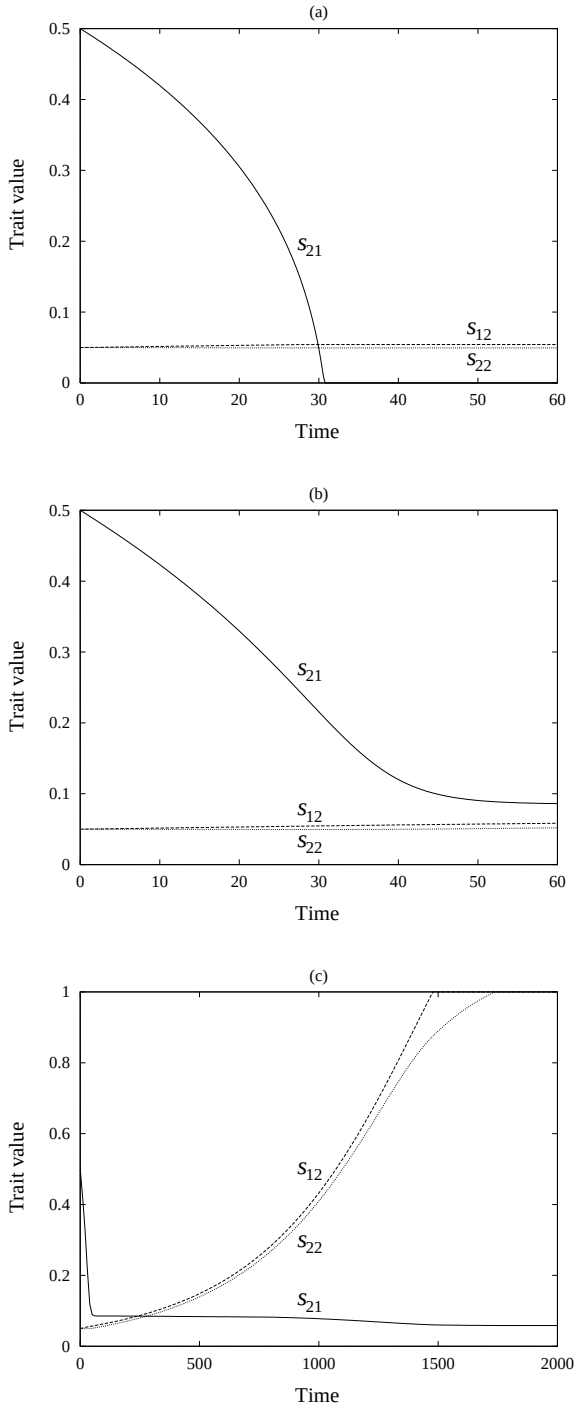

Figure 4. Evolution of trait s_{12} affecting resource transfer, and traits s_{21} and s_{22} affecting the probability of coupled births, in symbiosis: (a) without ($D_i = 1, \omega_i = 0$), and (b) and (c) with a cost ($D_i = 1, \omega_i = 10$) to evolution; s_{11} remains at zero throughout. Constants set as: $\alpha_i = 2$, $\beta_i = 1$, $\gamma_i = 10$, $\delta_i = 1$, $\varepsilon_i = 1$, e = 0.005, $\tilde{d}_i = 1$, $I_i = 10$, $g_i = 1$, $a_i = 0.002$, $\mu_{ij} = 0.001$, $\sigma_{ij}^2 = 0.001$.

The condition for invasion by a mutant s'_{i1}, causing a small increment to reproduction in the symbiotic state (and now an increment δd_i to mortality in the free-living state as well) is:

$$0 < \underbrace{\left(d_i(s_{i1}) - \hat{b}_i(s)\right)\cdot \delta\hat{\hat{b}}}_{I} + \underbrace{e\cdot \hat{n}_k(s)\cdot\left(\delta\hat{\hat{b}}_i + \delta\hat{\hat{b}}\right)}_{II} + \underbrace{\left(\hat{\hat{b}}(s_{i1}, s) - \tilde{d}_i - \tilde{d}_k\right)\cdot \delta d_i}_{III}. \qquad (8)$$

The exploiter, as before, remains at s_{11} = 0, and experiences no cost. In the victim two things happen. First, as s_{21} decreases, the victim's death rate in the free-living state increases, and term *I* becomes positive. Second, the increment in cost can become large enough for term *III* (which is negative) to come close to balancing terms *I* and *II*. Figure 4b illustrates the effect this has in arresting the downward trend of s_{21} before it reaches zero.

Such behaviour in trait s_{21} sets up the conditions needed for substantial increase in the rate of coupled birth events. Inequality (7) is replaced by

$$0 < \left(d_i(s_{i1}) - \hat{b}_i(s)\right)\cdot \delta\hat{\hat{b}} \qquad (9)$$

which, after some evolution, is now satisfied for the victim as well as the exploiter. Increased coupled births are now advantageous to both species, and there is a concerted shift towards a symbiotic unit capable of reproducing itself as a whole. This switch in direction of selection on the victim comes about, not through any benefit it gets from the exploiter, but because the costs associated with defence make the victim's free-living state less and less viable.

Figure 4c gives an example of this evolution. The early decline in s_{21} corresponds to that in Figure 4b. After this, both s_{12} and s_{22} increase, and continue to do so until they have both reached their maximum values. By time 1750, all births by the victim in the symbiotic state give rise to holobiont offspring. The same applies to most births by the exploiter, although the small remaining flow of resource from the victim to exploiter gives some excess offspring to the exploiter which are inevitably free-living. As one would expect, the rate of evolution of s_{i2} is of a lower order than

Table 1. Data for distinguishing between dependence and benefit of species in symbiosis.

		Model of symbiosis [1]		Viability of
		exploiter	victim	Amoeba clones [2] (%)
before evolution	partner absent	4500	4500	93
	partner present	7001	1154	
after evolution	partner absent	4500	212	7
	partner present	5482	2531	82

[1] Refers to abundance of species at equilibrium in the simulation in Figure 4c before evolution (time 0) and after evolution (time 2000).
[2] Summarizes information on the proportion of viable clones in an experiment on evolution of *Amoeba proteus* infected by bacteria (Jeon 1972).

that of s_{i1}; trait 2 does no more than redistribute a constant birth rate among free-living and symbiotic states, whereas the other trait affects birth and death rates directly.

Notice that large changes in abundance come about over the course of evolution. Equilibrium values at the start and end of the evolutionary process in Figure 4c are shown in Table 1; this gives both the total abundance in the presence of the other species, and the abundance that would be achieved if the other species were absent. The victim's free-living death rate becomes so high that this species can barely maintain a population at all in the absence of its partner.

It should be understood that the main results in this section, the invasion criteria in inequalities (6) to (9), are based simply on the ecological dynamics as described in equations (1) and Figure 2. The more detailed specifications of resource flow, density regulation and effects of phenotypic traits are needed for deriving the adaptive dynamics. But the invasion criteria themselves apply to much more general settings.

4. Discussion

The results above show that separate lineages can merge into symbioses capable of reproducing as a single unit even if resource transfer is entirely unidirectional from a victim to its exploiter. This happens if, in the course of developing defences against the exploiter, the costs experienced by the victim in the free-living state and the increments in these costs become sufficiently large. There is then a sustained shift in the symbiosis to reproduce as a single unit, and this maintains continuity of the association from generation to generation. The critical feature is that there should be more deaths than births in the free-living state (and correspondingly, less deaths than births in symbiosis) for both species; whether this is achieved by a mutualism, or by costs that one or other partner incurs in defending itself, is immaterial.

The holobiont that emerges as costs to the free-living individuals increase has a curious feature. To the physiologist concerned with resource flow between the partners, the association is clearly *not* mutualistic; the flow of resources is entirely unidirectional. On the other hand, to the ecologist, the symbiosis appears to be mutualistic; the partners satisfy the standard manipulation test for mutualism, because the abundance of each species falls when the other species is removed. Consider, for instance, the data on abundance after evolution in Table 1; association seems to be mutualistic, since both species are more successful in the presence of their partner.

To resolve this seeming paradox, it helps to distinguish between the properties of *dependence* and *benefit*, as suggested by Douglas & Smith (1989). A species can be said to have evolved greater dependence on its partner, if its abundance, when measured in the absence of its partner, decreases during the course of evolution with the partner. Table 1 shows that this happens to the victim, as this declines from an equilibrium abundance of 4500 to 212 as a result of its greater death rate when free-living; the exploiter, however, does not change. A species benefits from its partner after evolution, if its abundance in the presence of its partner after evolution is greater than it was in the absence of the partner before evolution. Table 1 shows that the outcome of evolution is to the benefit of the exploiter, as its abundance increases from 4500 to 5482, but not to the victim, as its abundance decreases from 4500 to 2531. The need to distinguish between dependence and benefit is evident in Jeon's (1972) study of *Amoeba*; from the

information on viabilities of clones summarized in Table 1, *Amoeba* clearly evolved dependence without any benefit (Jeon 1983).

In practice, it is usually hard to measure the extent of dependence and benefit, because experimenters rarely have access to the ancestral populations. But the existence of examples, such as those above, which show that dependence and benefit can be uncoupled, argues for caution in interpreting the status of longstanding symbioses (Douglas & Smith 1989). The symbiosis may not be beneficial to both partners in the sense above, and the manipulation experiments that ecologists might use after evolution to test for mutual benefit cannot prove it to be so (cf Law & Lewis 1983).

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Appendix: Derivation of a Macroscopic Evolutionary Dynamic

In this appendix we derive a dynamical system to describe the evolution of phenotypic traits in the symbiosis.

Microscopic time scale. The derivation begins at the smallest time scale of resource flux in and out of individuals; on this time scale abundance of the species and their trait values are constant. The rate of change of the internal concentration c_i of an individual of species *i* is given by:

$$\dot{c}_i = \alpha_i \cdot C_i - \beta_i \cdot b_i(c_i) + \left(\gamma_k \cdot c_k \cdot s_{k1} - \gamma_i \cdot c_i \cdot s_{i1}\right) - \delta_i \cdot c_i \qquad \text{(A1)}$$

where α_i, β_i, γ_i, and δ_i are rate constants for the flows as defined in Figure 1, $k \neq i$, and the term in large brackets applies only in symbiosis. Birth rate is proportional to the internal resource concentration: $b_i(c_i) = c_i \cdot \varepsilon_i / \beta_i$ where ε_i is a positive constant.

The internal concentrations at equilibrium can be obtained by setting the right hand side of equations (A1) to zero; this leaves expressions for the birth rates that depend on the external resource concentrations C_i. Since these concentrations become variables on the time scale of population dynamics, we write the birth rates as $b_1(C_1)$ and $b_2(C_2)$ for free-living individuals, $\tilde{b}_1(C_1, C_2)$ and $\tilde{b}_2(C_1, C_2)$ for offspring of symbiotic individuals that are born free-living, and $\tilde{b}(C_1, C_2)$ for those that are born into the symbiotic state.

Mesoscopic time scale. The equations below show the full dependence of population dynamics on external resource concentrations, and incorporate the dynamics of these resources:

$$\dot{n}_1 = +b_1(C_1)\cdot n_1 - d_1\cdot n_1 - e\cdot n_1\cdot n_2 + \tilde{b}_1(C_1,C_2)\cdot\tilde{n} + \tilde{d}_2\cdot\tilde{n} \quad \text{(A2a)}$$

$$\dot{n}_2 = +b_2(C_2)\cdot n_2 - d_2\cdot n_2 - e\cdot n_1\cdot n_2 + \tilde{b}_2(C_1,C_2)\cdot\tilde{n} + \tilde{d}_1\cdot\tilde{n} \quad \text{(A2b)}$$

$$\dot{\tilde{n}} = -\tilde{d}_1\cdot\tilde{n} - \tilde{d}_2\cdot\tilde{n} + e\cdot n_1\cdot n_2 + \tilde{b}(C_1,C_2)\cdot\tilde{n} \quad \text{(A2c)}$$

$$\dot{C}_1 = I_1 - g_1\cdot C_1 - a_1\cdot C_1\cdot(n_1+\tilde{n}) \quad \text{(A2d)}$$

$$\dot{C}_2 = I_2 - g_2\cdot C_2 - a_2\cdot C_2\cdot(n_2+\tilde{n}) \quad \text{(A2e)}$$

The vital rates in equations (A2a)–(A2c) are defined in Figure 2. Equations (A2d) and (A2e) describe the resource dynamics, and include a constant input rate I_i, loss due to uptake of resource *i* by individuals of species *i* with rate constant a_i, and loss from the ecosystem with rate constant g_i. All our numerical integrations of the system of equations (A2) come to equilibrium $(\hat{n},\hat{C}) = (\hat{n}_1,\hat{n}_2,\hat{\tilde{n}},\hat{C}_1,\hat{C}_2)$ (we have used fourth-order Runge-Kutta for the purpose).

Macroscopic time scale. Consider some point *t* in time on an evolutionary time scale. At *t* the resident populations are assumed to be monomorphic with respect to phenotype, the phenotypic state being denoted *s*, and the probability that the system is in state *s* being *P*(*s*,*t*). A mutant which escapes extinction when rare is assumed to go to fixation, the state of the system thereby undergoing a change: $s \to s'$. The rate of change of *P*(*s*,*t*) is written as

$$\frac{d}{dt}P(s,t) = \int\left[w(s\mid s')\cdot P(s',t) - w(s'\mid s)\cdot P(s,t)\right]ds' \quad \text{(A3)}$$

(van Kampen, 1992: 97), where $w(s\mid s')$ is the probability per unit time of the transition to s' for a system currently at state *s*.

A realization of this stochastic process can be thought of as a sequence of trait substitutions in the following sense (Metz *et al*. 1992). A mutation occurs for one of the traits in a community currently at equilibrium; if the mutant survives when rare, it spreads to fixation, causing a small change to the resident trait values and corresponding adjustments to abundance of the populations. A sequence of such mutation–survival–fixation events constitutes a trait substitution sequence. Repeating the whole trait substitution sequence over and over again, gives a bundle of realizations of the stochastic process, for which there is a mean path. The mean path is given by

$$\frac{d}{dt}s_y = \int (s'_{ij} - s_{ij}) \cdot w(s'_{ij}, s)\, ds'_{ij} \qquad , \tag{A4}$$

where $w(s'_{ij}, s)$ is the probability per unit time of the trait substitution $s_{ij} \to s'_{ij}$ (Dieckmann & Law 1996).

The probability per unit time $\mathscr{M}_{ij}$ of a mutant birth and the probability $\mathscr{S}_{ij}$ that the mutant survives extinction when rare are statistically independent, so we may take their product and write for trait *j* in species *i*

$$w_{ij}(s'_{ij}, s) = \mathscr{M}_{ij}(s'_{ij}, s) \cdot \mathscr{S}_{ij}(s'_{ij}, s) + \tilde{\mathscr{M}}_{ij}(s'_{ij}, s) \cdot \tilde{\mathscr{S}}_{ij}(s'_{ij}, s) \quad . \tag{A5}$$

Notice that mutants born free-living ($\mathscr{M}_{ij}, \mathscr{S}_{ij}$) have to be distinguished from those which are born into a symbiotic state ($\tilde{\mathscr{M}}_{ij}, \tilde{\mathscr{S}}_{ij}$), since both the probability of the mutant occurring and its chance of survival depend on this initial state. The mutation probabilities are

$$\mathscr{M}_{ij}(s'_{ij}, s) = \mu_{ij} \cdot M_{ij}(s'_{ij} - s_{ij}) \cdot \left(\hat{b}_i(s) \cdot \hat{n}_i(s) + \hat{\tilde{b}}_i(s_{ij}, s) \cdot \hat{\tilde{n}}(s) \right) \tag{A6a}$$

$$\tilde{\mathscr{M}}_{ij}(s'_{ij}, s) = \mu_{ij} \cdot M_{ij}(s'_{ij} - s_{ij}) \cdot \left(\hat{\tilde{b}}(s_{ij}, s) \cdot \hat{\tilde{n}}(s) \right) \qquad , \tag{A6b}$$

where μ_{ij} is the fraction of births which are mutants, and the mutant trait value is drawn from a probability distribution $M_{ij}(s'_{ij} - s_{ij})$ which is symmetric around s_{ij} with constant variance σ_{ij}^2 (the two traits in each species are assumed to be mutating independently). The term in large brackets in equation (A6a) (respectively (A6b)) gives the probability per unit time that a newborn individual appears in the free-living (respectively symbiotic) state.

To determine the probability that the mutant escapes extinction when rare, we employ a result from the theory of multitype branching processes based on the dominant eigenvalue λ and the corresponding left and right eigenvectors ($u = (u_1, u_2)$ and $v = (v_1, v_2)$ respectively) of the matrix L_i (equation 4b); see Athreya & Ney (1972: 184).

The probability that the mutant s'_{ij} does not ultimately become extinct is given by Theorem 1 of Athreya (1993) as

$$\mathscr{S}_{ij} = \lambda \cdot v_1 / \gamma \tag{A7a}$$

$$\tilde{\mathscr{S}}_{ij} = \lambda \cdot v_2 / \gamma \tag{A7b}$$

where

$$\gamma = b_i(s'_{ij}, s) \cdot u_1 \cdot v_1^2 + \tilde{b}_i(s'_{ij}, s) \cdot u_2 \cdot v_1 \cdot v_2 + \tilde{b}(s'_{ij}, s) \cdot u_2 \cdot v_2^2 \quad ,$$

the left eigenvector being normalized as $u_1 + u_2 = 1$, and the right eigenvector as $u_1 v_1 + u_2 v_2 = 1$. This result applies to mutations of small effect; if the mutant is able to increase, the branching process is said to be slightly supercritical.

Using equations (A5), (A6), (A7), and carrying out a Taylor expansion for small deviations s'_{ij} around s_{ij}, gives the deterministic path

$$\frac{d}{dt} s_{ij} = \frac{1}{2} \cdot \mu_{ij} \cdot \sigma_{ij}^2 \cdot \left(\mathscr{R}_i(s_{ij}, s) + \tilde{\mathscr{R}}_i(s_{ij}, s) \right) \tag{A8a}$$

The terms outside the large brackets come from the mutation process and scale the rate at which trait s_{ij} evolves; μ_{ij} is the fraction of births that are mutants and σ_{ij}^2 is the variance of the mutation distribution. The terms inside the brackets give the contribution to change in trait s_{ij} due to mutants which start as free-living ($\mathscr{R}_i$) and symbiotic ($\tilde{\mathscr{R}}_i$) individuals; these are:

$$\mathscr{R}_i(s_{ij}, s) = \left(\hat{b}_i(s) \cdot \hat{n}_i(s) + \hat{\tilde{b}}_i(s_{ij}, s) \cdot \hat{\tilde{n}}_i(s) \right) \cdot \frac{\partial}{\partial s'_{ij}} \mathscr{S}_{ij}(s'_{ij}, s) \Big|_{s'_{ij} = s_{ij}} \tag{A8b}$$

$$\tilde{\mathscr{R}}_i(s_{ij}, s) = \left(\hat{\tilde{b}}(s_{ij}, s) \cdot \hat{\tilde{n}}_i(s) \right) \cdot \frac{\partial}{\partial s'_{ij}} \tilde{\mathscr{S}}_{ij}(s'_{ij}, s) \Big|_{s'_{ij} = s_{ij}} \tag{A8c}$$

The first part of the right hand side of equations (A8b), (A8c) gives the rate at which offspring are produced; the second part is called a selection derivative (Marrow *et al*. 1993) and carries information about effects of traits on the ecological dynamics. For

mutations with small enough effects on the phenotype, equation (A8) is a good approximation to the mean path of evolution.