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# **Darwinian individuality and symbiotic associations**

Johannes Martens

## **Abstract**

Symbiotic associations (i.e. cooperative associations of heterospecific individuals) are often highly integrated and well-defined units. Yet, because of their intrinsic heterogeneity, it is unclear whether they should be granted with any sort of ontological status in evolutionary theory. In this paper, I address the related issue of their status as *Darwinian individuals*. To this end, I first distinguish the notion of a Darwinian individual from the notion of a unit of selection. I then envisage whether some symbiotic associations may fall under one or both of these categories. Finally, I conclude that instances of both types can be found in nature, and provide some criteria for this category-belonging.

## 1. Introduction

Symbiotic associations or symbioses, understood as cooperative organizations of *heterospecific* individuals, are widespread in the living world.<sup>1</sup> Up to now, several explanations have been proposed to explain the causes of their evolution—e.g. mutual benefits, reciprocity, or common reproductive fate (Sachs et al. 2004; Foster and Wenseleers 2006; Leigh 2010). But, despite these theoretical advances, the question of their ontological status has remained quite controversial in evolutionary theory. Recently, some philosophers of biology have proposed different perspectives on this problem (Sober and Wilson 1989, Queller & Strassmann 2009, Booth 2014, Clarke 2016, Godfrey-Smith 2015). This paper intends to bring a further contribution to this debate.

Two reasons (at least) can be invoked to explain the conceptual *indeterminacy* which surrounds the ontological status of symbioses in the Darwinian theory. First, the very notion of symbiosis does not refer to a homogenous class of entities, but rather to a heterogeneous *continuum* of associations—which exhibit a great deal of variation in both their reproductive and functional structures (thus, a flower plant/insect pollinator mutualism is certainly very different from a host-symbiont mutualism with respect to both of these aspects). Second, the very entities to which this notion refers to are by definition *heterogeneous* entities, i.e. entities that are made of parts which pertain to different species. Thus, because of this constitutive heterogeneity, one could wonder whether they should be granted with any kind of ontological status in evolutionary theory (e.g. the status of unit of selection).

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<sup>1</sup> In this paper, the notion of symbiotic association (or symbiosis) will be used to refer to a subcategory of the more general class of mutualisms (West *et al.* 2007). In a mutualism, the multiple partners can *either* belong to different species *or* belong to the same species; but all of them derive some kind of benefits from their mutual interaction. These benefits do not have to be *direct* benefits, however (cf. section 4).

In this paper, I will address these two aspects of the “indeterminacy problem” by distinguishing between three kinds of symbioses—which roughly correspond to the different places of the “continuum” mentioned above—namely (i) those where all the selection takes place at the level of the symbiotic partners, (ii) those where the symbiosis itself counts as a unit of selection (with heritable variation in fitness), and (iii) those which can be envisaged as Darwinian individuals. As I will show, the latter kind is certainly the most puzzling, for Darwinian individuals—at least in the acceptance that will be adopted here—usually refer in the literature to biological individuals whose parts have somehow “*renounced*” to their own reproductive success.<sup>2</sup> Yet, it is unclear *how* biological entities that do not belong to the same species could “renounce” to their reproductive success in favour of their heterospecific associates (Hamilton 1964). Rather than eluding this point, I will provide some evidence that (some) endosymbioses can in fact satisfy this *prima facie* counterintuitive requirement.

The structure of this paper goes as follows. In section 2, I address the question of whether some symbiotic associations deserve the status of unit of selection. In sections 3, 4, and 5, I address the question of whether some symbiotic associations deserve the status of Darwinian individuals (Darwinian individuals, in the view defended here, constitute a *kind of* unit of selection). Section 3 introduces the definition of Darwinian individuality by emphasizing two necessary conditions that are (usually) associated with it, namely the existence of strong altruism among the parts, and the existence of mechanisms of control guarantying the existence of a heritability at the symbiotic level. Section 4 develops an argument showing that strong altruism—i.e. *self-sacrificial* behaviours—can actually evolve between members of different species, though in a somewhat indirect way, while section 5 address two cases of host-symbiont

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<sup>2</sup> One advantage of this definition is that it fits well with the metaphysical definition of individuality (Chauvier 2016), and more specifically with the criterion of formal indivisibility—according to which an individual (e.g. a dog or a unicell) cannot be *formally* composed of individuals of the same kinds.

relationships that could be envisaged as *bona fide* exemplars of Darwinian individuals (viz. with both strong altruism between their members and symbiotic heritability).

## 2. Symbioses as units of selection

According to its most popular definition (Lewontin 1970), a “unit of selection” refers to a member of a biological population that exhibits variations (or at least a potential for variations), fitness differences, and heritability. Taken individually, these properties can be envisaged as *necessary* conditions for the occurrence of natural selection. However, several issues arise when we consider their application at the level of symbiotic associations. In this section, I will focus (exclusively) on the last two of them, namely fitness and heritability.

To begin, it is important to distinguish between two ways of measuring the fitness of biological collectives (Damuth and Heisler 1988)—which include (by definition) the symbiotic associations. Following a terminology popularized by Okasha (2006), I will refer to these measures as collective fitness 1 and collective fitness 2 (hereafter abridged W1 and W2, respectively). Collective fitness 1, on the one hand, is a measure of the overall productivity of a given collective, and can be defined as the average number of individual particles<sup>3</sup> produced throughout its lifetime. Collective fitness 2, on the other hand, is a measure of the number of collectives produced by a given collective, and—unlike the former—does not necessarily depend on the average fitness of its component particles.<sup>4</sup>

In the evolutionary literature, W2 is typically associated with the idea of collective *reproduction*, whereas W1 is more associated with the idea of collective *productivity* (reproduction, in this latter case, takes place at the level of individual particles). However, both

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<sup>3</sup> “Particle” is just a neutral term used by Okasha to denote a member of a biological collective (e.g. a cell in a multicellular organism, a zebra in a herd, an alga in a lichen, etc.).

<sup>4</sup> Indeed, the two measures are logically independent, though they may be (in some cases) causally related.

of these measures are equally legitimate to describe the action of natural selection in a multilevel setting. In general, W1 provides a useful measure of collective fitness when one is trying to explain the evolution of a particle character in a structured population, like the evolution of a sex-ratio or the evolution of a cooperative behavior, whereas W2 constitutes a more appropriate measure when one is trying to explain the evolution of a collective character—like a pattern of cell specialization or a degree of functional integration. But, ultimately, the applicability of these measures depends on the *mode of development* of the collective one is considering, namely unitary or aggregate (Queller 2000).

With a *unitary* development, i.e. a population of collectives each formed by a single propagule, both W1 and W2 measurements can be applied. But W1 can sometimes yield incorrect estimations of evolutionary success. For instance, in a population of multicellular organisms who possess a reproductive division of labour between a somatic line and a germ line, using average cell fitness (e.g. average division rate) as a measure for collective fitness may lead to an incorrect prediction of the evolutionary dynamics. This is because the differences in the number of propagules produced by their germ line (W2) won't necessarily be correlated with the former. So W2, in this case, is more appropriate.

With an *aggregate* development (i.e. a population of collectives each formed by the aggregation of propagules from different “parental” collectives), both measurements can in principle be applied. But in practice, W2 will often be intractable, and even wholly inadequate. To illustrate this point, imagine a small population of collectives in which *each* collective from the parental generation contributes to the formation of *all* of the collectives in the offspring generation (this can happen if all of the particles released by the “parental” collectives are mixed in a global pool and used to reform the next generation of collectives). In this scenario, all of the parental collectives have an equal W2, which is equal to the total number of collectives in the next generation. But, despite the absence of differences in W2, the respective W1 of the

collectives in the parental generation—defined as their average contributions to the composition of the offspring collectives—could be very different (Okasha 2001). Specifically, if it turned out that the evolution of their internal composition, e.g. the proportion of a given type of particle, was a function of their difference of productivity (number of propagules produced), focusing on the differences in collective reproduction would amount to overlook a key determinant of their structure.

In the case of symbiotic associations, the distinction between a unitary and an aggregate mode of development is mirrored by the distinction between two modes of symbiosis formation, namely perfect co-dispersal and separate co-dispersal of the partners. With a perfect co-dispersal of the partners (like with an obligate transmission of the symbionts), parent-offspring lineages can be directly identified at the symbiotic level, and the count of W2 is unproblematic. However, when the partners of a multispecies association are not perfectly co-dispersed, intractability of W2 is the norm; for the absence of co-dispersion generally prevents the identification of clear patterns of ancestry at the symbiotic level (Sterelny 2011; Godfrey-Smith 2011).

This point can be illustrated by considering the symbiosis between the Hawaiian bobtail squid *Euprymna scolopes* and its symbiotic bioluminescent partner *Vibrio fischeri* (Bouchard 2010; Booth 2014). In this symbiosis, the squids acquire their bacterial symbionts from the surrounding waters at an early stage of their development, and the symbionts are then hosted in a dedicated organ where they generate bioluminescence. Bioluminescence is highly valuable to the squid, as it provides her with a night camouflage from the predators located below in the water column (thanks to it, the squid is no longer visible as a black spot in the moonlight). But the *Vibrio* lineages also benefit from this process, thanks to the squid's light organ, which provides them with a shelter to grow and expand rapidly (Visick & McFall-Ngai 2000). Overall, the squid-*Vibrio* symbiosis forms a clear adaptive unit—which relies on both mutual

benefits and a tight physiological dependency. Yet, despite these mutual benefits, the whole association cannot be envisaged as an entity which reproduces itself (not at least, in the ordinary, “non-marginal” sense of the term), for the fates of the different lineages involved in this particular interaction are not perfectly intertwined—indeed, the *Vibrio* lineages are horizontally transmitted, and their number may vary from squid to squid. For this reason, there is no clear parent-offspring lineages at the level of the squid-*Vibrio* collectives, and W2 does not constitute an appropriate measure of symbiotic fitness.

Intractability of W2 is certainly a good reason for not granting the status of “reproducer” to a symbiotic association (sensu Griesemer 2000; Godfrey-Smith 2009). But W2, as we have seen, is not the only possible way of measuring the fitness of a collective entity. Indeed, another possibility (in cases where W2 is not readily applicable) consists in defining the fitness of an association using W1, i.e. its average productivity, all lineages included.

At first, the choice of W1 as a measure of symbiotic fitness could seem appropriate to account for the many cases of “community selection” that have been reported in the literature—e.g. selection at the level of phoretic associations (Sober and Wilson 1989). But this measure is rather problematic, for symbiotic associations are, by definition, *heterogeneous* entities, that is, entities whose parts do not (in general) belong to the same Darwinian population; and, because of this intrinsic heterogeneity, it is usually impossible to model the evolutionary dynamics of these associations by computing the aggregate fitness of all the lineages within them.

In the squid-*Vibrio* symbiosis, for instance, both partners face shared selection pressures (e.g. avoiding being eaten by a predator during the symbiotic phase) as well as strong idiosyncratic selection pressures; and admittedly, the latter remain too important to consider the whole association (i.e. the squid plus the different strains of *Vibrio*) as a homogeneous group—namely as a group whose fitness would be adequately measured by a single, aggregate metric. In this case, the best approach is thus to compute separately the average fitness W1 of the



different lineages, and to interpret the evolutionary dynamics at the symbiotic level as a case of co-evolution.

Heterogeneity, however, is a matter of degree. Thus, at an ecological scale, two individuals may well pertain to different species, and yet share a significant number of selective pressures that affect several important aspects of their life. Besides, at a phenotypic/genotypic scale, two heterospecific individuals may well exhibit important similarities due to common descent, and/or be involved in close genetic interactions that contribute in homogenizing multiple aspects of their phenotype. Ideally, all of these dimensions (ecological, phenotypic and genotypic) should be combined in a single scheme that may be used to determine the extent to which two individuals are “*exchangeable*” (Matthewson 2015) or “*fungible*” (Queller 2000) in the same Darwinian population. But concretely, few multispecies communities are likely to be sufficiently homogeneous—according to such an ideal criterion of exchangeability—to justify the use of W1 as a measure of symbiotic (collective) fitness.

Surely, one of the best candidates to the status of “bearer of a W1” are multispecies bacterial biofilms. In those associations, lateral gene transfer (i.e. the exchange of genes between different strains of bacteria) ensures a non-negligible amount of phenotypic and genetic exchangeability (Ereshefsky and Pedroso 2013) and also plays a key role in several aspects of their collective development—like the defence of the biofilm against host antibiotics. Yet, as Clarke (2016) recently argued, lateral gene transfer does not promote a global homogenization at the level of bacterial strains, and so is probably not a sufficient reason for ascribing a W1 to the whole biofilm. Specifically, Clarke argues that

“the extent to which lateral transfer could act as a homogenizing influence on biofilms is limited by the fact that transfer is trait-specific. It will not bring about the sort of across-trait relatedness that occurs as a consequence of common descent. Cooperation

between cells that are related only at a single locus is expected to be unstable because it can act against the interests of all the other genes of those cells. They have a common evolutionary fate with respect to just one out of many traits, in other words.” (p.207)

Thus, due to the local character of lateral gene transfer, it is unlikely that multispecies biofilms will count as a unit of selection. But for this same reason, it is even more unlikely that other symbiotic associations (with less “exchangeable” partners) will possess a sufficient amount of homogeneity to count as a unit of selection (in the W1 sense).

The intrinsic heterogeneity of symbiotic associations is also problematic when one tries to compute the heritability of symbiotic characters at the higher level. Like collective fitness 1 and 2, collective heritability can be declined into two different measures (Okasha 2006), whose application depends on the mode of development of the collectives one is considering—namely aggregate vs. unitary. Heritability 1 is an aggregate measure of heritability, derived from the heritability coefficients at the level of particle lineages, and can be used to measure the similarity between the composition of a collective and the composition of the set of particles it produces (e.g. the frequency of cooperators cells in a multicellular aggregate and the frequency of cooperators cells in the set of propagules it produces at the end of its life-cycle). Heritability 2, in contrast, measures the character similarity at the collective level, and takes the individual collectives as the relevant units for measuring this similarity.

With a unitary development, both W2 and heritability 2 can be used to describe the evolution of character, assuming some form of collective selection, whereas, with an aggregate development both W1 and heritability 1 are the appropriate measures. However, in the case of multispecies collective, the genetic patterns of transmission of particle characters (e.g. strains of bacteria, or a host and its microbiota) are often very specific to the species involved, which renders—in practice—the computation of heritability 1 impossible. Specifically, applying a

single measure of heritability at the aggregate level requires that the phenotype at the particle level as well as its pattern of transmission are sufficiently homogeneous. But often, a co-evolutionary approach (with separate heritability coefficients) will be more appropriate.

### 3. Symbioses as Darwinian individuals

Up to now, I have emphasized two important issues related to the satisfaction of Lewontin's conditions at the level of symbiotic units, namely (i) the intractability of W2 (due to an imperfect co-dispersal of the partners) and (ii) the heterogeneity of symbiotic associations (envisaged as an obstacle to the use of W1 at their level). In this section (and the next ones), I will address a more specific—though related—problem, namely: the recognition of some symbiotic units as *Darwinian individuals*.

In the philosophical literature, the notion of Darwinian individual is sometimes used interchangeably with the concept of unit of selection. But this assimilation is, I think, misleading, for the notion of Darwinian individual is typically associated with stronger conditions and/or properties that are not *part* of the definition of a unit of selection (Buss 1987; Michod 2000, 2005; Okasha 2006). Thus, Darwinian individuals (such as bacteria, cats and oaks) are often considered as entities who are able to reproduce themselves—that is, as entities who are able to produce more entities of their own kind (W2)—though this criterion is clearly not required for a collective to be considered as a unit of selection.<sup>5</sup> Furthermore, Darwinian individuals are typically envisaged (in this stronger sense) as entities whose component parts are no longer able to reproduce by themselves.<sup>6</sup> So, if one wants to determine whether some

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<sup>5</sup> Indeed, many entities that satisfy Lewontin's conditions, such as groups of cooperating insects or animals, are unable to reproduce in this way, and can only evolve new collective characters through the reproduction of their individual components (i.e. by an increase of their productivity W1).

<sup>6</sup> This contrasts with the existence of many social groups which satisfy Lewontin's conditions, but whose component particles retain the ability to reproduce directly.

symbiotic entities could satisfy the (stronger) conditions that are traditionally associated with the concept of Darwinian individual, one needs to start by distinguishing the latter from the (more general) notion of unit of selection.

The distinctive properties of Darwinian individuals are traditionally envisaged within the framework of the “major” transitions theory in evolution (Calcott and Sterelny 2011). According to this theory, a transition in evolution is an event during which a higher level of Darwinian individuality (e.g. multicellular individuals) *emerges* from the aggregation and cooperation of lower level entities (e.g. unicellular creatures) under the action of natural selection. Once a transition is achieved, the entities at the lower level no longer “enjoy” a reproductive autonomy, and their evolutionary fate cannot be dissociated from that of the newly emerged individual. This “renouncement” of the lower entities to their own reproductive success—together with the emergence of a collective reproduction at the higher level (in a W2 sense)—constitutes the hallmark of a transition event (Michod 2005; Okasha 2006; Godfrey-Smith 2009). It also provides, at least *prima facie*, a useful criterion to distinguish “genuine” Darwinian individuals from “mere” biological societies—namely: the former are actual units of selection that are *not* themselves made of actual units of selection.

Three steps or conditions can be reasonably thought of as *necessary* for the completion of a transition in individuality, so understood. First, collectives must form parent-offspring lineages; for otherwise, it is not possible to ascribe a W2 to each of the collectives—and thus, not possible to compute the heritability coefficient for collective characters. In order to be satisfied, this condition requires the evolution of a unitary mode of development at the collective level,<sup>7</sup> but also the existence of sufficiently delineated collectives to serve as units of selection (Godfrey-Smith 2006).

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<sup>7</sup> The evolution of a development in “bottleneck” (i.e. through a *single-celled* stage) can help, but is not necessary.

The second step for the emergence of a new level of individuality is the *decoupling* between W1 and W2 at the group level (Michod & Nedelcu 2003; Michod 2005; Okasha 2006). Put simply, this condition means that, once a transition has occurred, W2 must no longer be proportional to W1—the average fitness of the lower level particles. To illustrate it, one may compare the evolutionary fate of groups that have evolved a reproductive division of labour with the fate of those groups where all the members retain their reproductive rights. In the latter case, the number of “propagules” (W2) produced by a given collective is always proportional to the average reproductive success of the members. So there is no relevant distinction between the productivity of the collective and its reproduction (number of propagules produced). By contrast, in presence of a reproductive division of labour,<sup>8</sup> this relation of proportionality is no longer guaranteed, and W2 is usually the main determinant of the evolutionary dynamics at the collective level.

Most of the time, cooperation among particles guarantees a high level of functional integration within groups, which in turn increase their W2. But “mere” cooperation is not sufficient for the decoupling between W1 and W2; for, in many instances, the evolution of cooperative traits at the particle level can be explained *as well* by the maximization of W1 at the collective level. For instance, a group composed mostly of cooperative members may well be the fittest according to both the maximization of W2 and W1; but in this case, the decoupling between W1 and W2 doesn’t occur. In fact, in order for a proper (unambiguous) decoupling to occur, what is required is the evolution of *strong altruism*, i.e. the evolution of self-sacrificial behaviours at the lower level (like with somatic investment or eusocial behaviours); for it is only with this kind of investment that a lower-level particle can become a *part* of a broader Darwinian individual—by “renouncing” to its whole reproductive success.

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<sup>8</sup> This also includes those entities, like plants, whose development does not involve an *early* germ-line segregation.

The third step toward the emergence of a new level of Darwinian individuality is intimately related to the second one, and concerns the decoupling between *heritability* at the collective level (i.e. the fidelity in the transmission of collective characters) and *selection* at the particle level. Unlike the case of the decoupling between W1 and W2, this third step doesn't require the evolution of strong altruism, but the existence of mechanisms which prevent selection at the lower level from subverting the stability of adaptations at the group level.

Taken together, these three conditions embody a clear schema of Darwinian individuality at the level of collectives. But the question is: do they also apply to some symbiotic units? With respect to this problem, the first of our three conditions (i.e. the evolution of parent-offspring lineages at the collective level) is certainly the least problematic; for, provided there is a strict co-dispersal of the symbionts, a collective reproduction W2 will automatically emerge at a symbiotic level. And, though the identification of such lineages can be difficult in practice (as we saw in section 2), the realization of this condition, in principle, is not really an issue. The realization of the second and third conditions, however, raises more delicate problems—on which I will now turn.

The decoupling of W1 and W2, together with the decoupling of heritability and selection at the collective and the particle level, are two essential steps in the constitution of a higher level of Darwinian individuality. Yet, both of these steps actually imply that the particles at the lower-level have *renounced* to their evolutionary potential, that is, to their status as Darwinian individuals.

The decoupling between collective heritability and particle selection (condition 3) occurs when the evolutionary success of the particle within groups is entirely aligned with the success of their group, so that any form of reproduction at the lower level becomes a function of growth or development at the collective level.<sup>9</sup> Godfrey-Smith (2009) describes this process with the

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<sup>9</sup> Otherwise, it is wiped out by collective selection, as in the case of tumoral cells.

term “de-Darwinization”, which corresponds to the point where the intrinsic properties of the lower-level particles cease to be correlated with their long-term evolutionary success. Usually, de-Darwinization is enforced in multicellular collective by evolved mechanisms such as an early germ line segregation or an immune system. But, in order for these mechanisms to result in a proper *transfer* of fitness from the lower level to the higher level (Michod 2005), a decoupling between W1 and W2 is also required (condition 2); for only the latter guarantees that the newly emerged individual won’t be merely a by-product of selection at the lower level.

As mentioned above, this second decoupling requires the evolution of strong altruism at the particle level. But the problem with symbiotic units is then the following. Unlike the traditional examples of Darwinian individuality—e.g. multicellular organisms or eusocial insects—symbiotic associations are made of entities which, by definition, are *not* genetically related; yet, as is well-known, positive relatedness *is* a necessary condition for the evolution of strong altruism (Hamilton 1964; Gardner *et al.* 2011). Specifically, the condition for the evolution of strong altruism is given by the classical version of Hamilton’s rule, namely  $rb - c > 0$ , where  $r$  denotes the coefficient of genetical relatedness,  $b$  the indirect benefits of altruism, and  $c$  the absolute fitness cost to the altruist. But, between members of different species, the relatedness coefficient  $r$  equals zero—which, seemingly, implies that strong altruism cannot evolve in mutualisms. Thus, if we accept that strong altruism is required for the proper constitution of a Darwinian individual, the question becomes: should we deny this qualification of Darwinian individual to all symbiotic associations?

In sections 4 and 5, I will argue that some symbiotic associations can actually count as Darwinian individuals *in this particular sense*. But some readers would certainly prefer to avoid this difficulty by rejecting our antecedent (i.e. the claim that “strong altruism is required for the emergence of a Darwinian individual”) and instead, argue for a weaker definition of what a Darwinian individual is.

Recently, O'Malley & Powell (2016) have criticized the theoretical framework about the “evolutionary transition in individuality” on the basis that it doesn't say much about symbiotic events, such as the evolution of the eukaryotic cell or the acquisition of plastids. This is undoubtedly a theoretical limitation of this approach; but it is not very surprising; for the sort of strong altruism which actually promotes the decoupling between W1 and W2 (e.g. in the transitions toward multicellularity and eusociality) is *not* observed in the event that have led to the emergence of the eukaryotes through the fusion of two prokaryotes.

In order to account for this type of event—and more generally, for the emergence of multispecies Darwinian individuals—the most common alternative is to opt for a weaker account of the notion of transition toward individuality. Queller (1997), for instance, distinguishes between two types of transitions, namely “fraternal” and “egalitarian”. In a fraternal transition, a higher level unit evolves through the operation of kin selection and emerges on the altruistic cooperation of the lower level entities (like the ants of an ant colony), whereas in an egalitarian transition, it is the cooperation of *unrelated* entities that leads to the emergence of a functional whole (e.g. the physiological integration of a host and its symbionts). According to him, both of these transitions have in common the fact that the emerging entities (i) have the capacity to form lineages and (ii) exhibit a high degree of functional integration. So his notion of transition can accommodate both symbiotic and fraternal entities within the same concept of Darwinian individual. Yet, one may question whether (i) and (ii) really suffice to distinguish Darwinian individuals from other kinds of biological units—such as units of selection or biological societies.

Take property (i) for instance. Property (i) is a property that is both satisfied by multicellular organisms and by species (Hull 1978). But clearly, the kind of mereological dependency that relates a species' W2 to its component parts is very different from the kind of dependence that relates a multicellular organism's W2 to its component cells. So the existence of parent



offspring lineages cannot be a sufficient condition to count the connected entities as a Darwinian individuals.

Functional or reproductive integration (ii) is also a distinctive property of many Darwinian individuals. But likewise, I do not think that this property should be viewed as central to the definition of Darwinian individuality. Godfrey-Smith (2015) takes it to be the most important factor in the transition toward the evolution of collective reproducers.<sup>10</sup> More precisely, Godfrey-Smith claims that the key to the transition toward a new level of Darwinian individuality is not the complete renouncement to reproductive success, but rather the *externalization* of the reproductive abilities—what he calls “scaffolded reproduction”. According to his perspective, a particle will become a part of a broader Darwinian individual when it is no longer able to synthesize all of the required components to reproduce by itself (e.g. a mitochondria in a cell). So, in this respect, both a cell in a multicellular organism or a plastid in a eukaryotic cell can be envisaged as parts of a broader reproducer.

The merit of this definition is that it provides, *prima facie*, a unified basis for understanding both fraternal and egalitarian transitions with a single criterion (“scaffolded reproduction”, or the loss of reproductive autonomy). But this criterion, in my view, is too broad to neatly single out the set of Darwinian individuals, for it also include some associations whose status as Darwinian individual is highly debatable. For instance, many sexual organisms cannot reproduce without the contribution of their partner; and yet there is not much in common between (say) a multicellular organism and a pair of sexual individuals—at least not much that would justify the use of a single concept of Darwinian individuality for these different entities. To take another example: retrovirus (and probably many obligate parasites) cannot reproduce without using the molecular machinery of the host cells; yet it would be doubtful, if not meaningless, to envisage the parasite/host pairs as Darwinian individuals.

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<sup>10</sup> The other factors taken into account by Godfrey-Smith are the presence/size of a bottleneck and the degree of germ/soma separation.

I would also stress that the kind of functional integration put forward by these authors is more a mark of *organismality* than of Darwinian individuality. These properties of biological collectives are often conflated in the evolutionary literature, but it is important to keep them distinct (Godfrey-Smith 2009; Pradeu 2016): the former is an *actual* property of some entities with a high physiological integration among their parts, the second is more a *disposition* of some units (Clarke 2013), and is better envisaged as a cause of the evolution of functional cohesiveness at the level of biological collectives.

Now, if we reduce the emergence of Darwinian individuality (involving the decoupling of W1 and W2) to the “fraternal” transitions (Queller 1997), what remains to be done is, first, to see how strong altruism can evolve between species, and second, how this disposition of the lower-level units can be generalized and maintained within the symbiotic collectives. This second condition corresponds to the decoupling between lower-level selection and heritability at the level of the symbiotic unit described earlier. I address both of these points in sections 4 and 5, respectively.

#### **4. Altruism between species**

At first, to claim that strong altruism can evolve between members of different species may sound as a contradiction in terms. In this section, I will show that kin selection theory has actually the resources to explain how this might happen. But before that, I would envisage another theoretical framework that has been proposed to account for this (curious) possibility. Known as the “direct fitness approach”, this alternative framework relies on a simple but rather thought-provoking idea, which is that phenotypic assortment, *not* genetic relatedness, is the key to the evolution of altruism (Fletcher and Doebeli 2006, 2009).

One interesting illustration of this perspective has been given by Fletcher and Doebeli (2009), who devised an ingenious thought experiment to “demonstrate” that strong altruism can evolve without positive relatedness. Fletcher and Doebeli’s thought experiment goes as follows. Suppose a large population of haploid bacteria where two types of individuals coexist, namely altruistic and selfish individuals. Altruism, in this population, consists in the production of a common good, i.e. a specific enzyme, which can be activated through two independent regulatory mechanisms. The first mechanism is activated when the individual possesses the allele A at a (bi-allelic) locus L1, while the second mechanism is induced by the possession of the allele B at a second (bi-allelic) locus L2. The possession of either allele a at L1 or b at L2 neither induces nor inhibits the activation of these mechanisms; but the possession of *both* A and B systematically entails the death of the individual (due to the overproduction of a toxic metabolite). Hence, there are three viable genotypes, namely Ab, aB and ab, but only two phenotypes, altruism and selfishness.

In this model, reproduction is clonal and interactions are pairwise. Fletcher and Doebeli also assume that each interaction corresponds to a simple, additive prisoner’s dilemma. But the key to their scenario lies in the pattern of assortment. More specifically, these authors assume that an experimenter imposes the *strongest* form of assortment between individual bacteria, but in such a way—and it is the crucial point—that carriers of the same altruistic allele *never* interact with other carriers of this allele. Thus, in the population, unrelated altruists always end up together (forming Ab/aB pairs); whereas clonal egoists always end up together (forming ab/ab pairs).

Because of this specific pattern of interaction, altruism inevitably ends up by dominating the whole population. But what is interesting here is the *explanation* advanced by Fletcher and Doebeli to account for this outcome:

“[In this model], the help which carriers of A provide never goes to other carriers of A and the help that carriers of B provide never goes to other carriers of B. Thus, even though cooperation evolves, it does not evolve due to kin selection (genetic similarity among those that interact). Instead, it evolves owing to assortment between phenotypic cooperators. More precisely, cooperation evolves because carriers of cooperative alleles, whether A or B, receive help from cooperative phenotypes, not from other carriers of the same allele.” (p.16)

In another passage, Fletcher and Doebeli claim that direct, and not indirect benefits, are the key to understand the evolution of strong altruism: “direct fitness benefits can, and indeed must, explain the evolution of (‘strong’) altruistic cooperation.” (ibid.). Thus, according to these authors, the direct fitness approach provides a better causal interpretation than kin selection hypothesis.

Fletcher and Doebeli insist on the “logical strength” of their thought experiment. Yet, there are three possible objections one may address to their interpretation.

A first possible objection one could make is that the trait they are considering is *not* genuinely altruistic—at least, not in the “strong” sense of the term. However, I do not think that this objection is receivable. At first, if one looks at the nature of the interactions within the pairs of altruists, the dimension of “self-sacrifice” is not obvious; for both Ab and aB individuals receive help from their partner during the course of the interaction. But “not obvious” doesn’t mean “non-existent”; and in fact, it is easy to check that the nature of the cooperative trait considered by these authors involves a true (though implicit) dimension of sacrifice. To see it, all one has to do is to take an altruist individual within a pair of altruists, switch its phenotype to selfishness—all things being equal, including the type of the partner—and then observe the consequence of this change on its fitness. Because the game played by the individuals

correspond to a prisoner's dilemma, this consequence will be a net increase in absolute fitness. So the altruistic nature of the trait is corroborated.<sup>11</sup>

Another possible objection one could address to their argument concerns the way these authors define the relatedness within the pairs of altruists. This objection has been formulated by Gardner *et al.* (2011):

“Fletcher & Doebeli (2009) [in their model] incorrectly calculated the coefficient of genetic relatedness, treating it as a measure of genotypic similarity *per se*, rather than a measure of genetic similarity. Although social partners under their unusual pairing scheme carry different alleles at both of the loci underlying the altruistic trait, their genetic predisposition for altruism is exactly the same, and hence the coefficient of genetic relatedness is unity ( $r = 1$ ), and not zero ( $r = 0$ ) as Fletcher & Doebeli (2009) suggested.” (Gardner *et al.* 2011, p.1035)

By genotypic similarity *per se*, Fletcher and Doebeli mean molecular similarity. But molecular similarity, Gardner *et al.* argue, is not something the evolutionists are interested in. In contrast, evolutionists are primarily interested in phenotypic evolution; and in the case devised by Fletcher and Doebeli, the phenotype of both aB and Ab individuals is *the same* (i.e. the production of the same enzyme). So, rather than considering relatedness as a measure of allelic similarity, one should consider it, according to Gardner *et al.*, as a measure for the heritable portion of the altruistic phenotype, from which it follows that ( $r = 1$ ).

I have to say that I'm broadly sympathetic with this argument. But I do not find it fully satisfying, especially if our aim is to understand how altruism could evolve between members of different species. In Fletcher and Doebeli's scenario, the phenotype is *homogeneous* across Ab and aB individuals, and reproduction is clonal. Thus, all of the individuals in this population

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<sup>11</sup> Alternatively, one could as well switch the phenotype of a selfish individual into that of an altruist individual, observe that this individual incurs an absolute fitness cost, and reach the same conclusion.

of bacteria satisfy the criterion of “exchangeability” briefly alluded to in section 2—at least at the phenotypic level.<sup>12</sup> But exchangeability, as we have seen, is a matter of degree; and as we will now see, it is easy to devise a similar case where, even though the trait that evolve between partners is (without doubt) strongly altruistic, a homogeneous criterion of relatedness is not applicable.

To give only one representative example, imagine a situation where the population structure is the same as in Fletcher and Doebeli’s scenario (reproduction is clonal, interactions are pairwise, and an experimenter imposes a perfect assortment between individuals with the altruistic phenotype), except that altruist and selfish individuals now belong to different species with different lifestyles and completely heterogeneous phenotypes. In this modified version of their thought experiment, altruists of species 1 always interact with altruists of species 2, and egoists of species 1 always interact with egoists of species 2. So, like in the previous scenario, altruism goes to fixation in each population. Yet, there is an important difference here. Ultimately, if we want to account for the evolution of this trait, we *cannot* assume that relatedness is equal to unity, for in this example, the phenotypes of the two species do not have enough homogeneity to justify a common unit of measure for their heritability in fitness (barring the obvious differences in their genotypic basis). In fact, arguing for the contrary would amount to embrace Fletcher and Doebeli’s position—which puts phenotypic assortment, not relatedness, to the centre stage.

How, then, should we account for the evolution of the altruistic phenotypes in Fletcher and Doebeli’s scenario? For these authors, the explanation is simple: strong altruism evolves thanks to the direct benefits generated by phenotypic assortment. Yet, there is an alternative explanation which, though acknowledging the absence of positive relatedness within pairs, remains in accordance with kin selection theory. Put simply, the idea is that there *are* indirect

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<sup>12</sup> In other words, it is reasonable to envisage them as parts of the same Darwinian population.

benefits in the previous thought experiment, but that they are not represented by the classical form of Hamilton's rule. To account for these indirect benefits, one needs to consider *all* the relevant effects of a given altruistic behavior on the fitness components of different kinds of relatives, which comprises the long-term indirect benefits received by those relatives who live in distant generations.

To establish the role of indirect benefits in Fletcher and Doebeli's scenario, let's imagine what would happen to a focal altruist with a genotype  $Ab$  or  $aB$  in a given pair if she mutated into a selfish individual with genotype  $ab$  (*ceteris paribus*).<sup>13</sup> First, her mutation would leave unaffected the value of relatedness within the pair; for relatedness, in this scenario, is equal to zero. Second, mutating into a selfish individual would have the effect of raising (*ceteris paribus*) the direct fitness of the mutant, i.e. the number of offspring that it can itself produce, freeing it from paying the cost of producing the enzyme. But most importantly, mutating into a selfish individual would have the effect of *modifying* the genotype of the mutant's own offspring—according to the clonal pattern of heritability—and this, in turn, would affect negatively their evolutionary success (“condemning them”, so to speak, to interact exclusively with selfish individuals).

Hence, in Fletcher and Doebeli's scenario, the ultimate recipients of altruism (i.e. the recipient at the end of the causal chain) are *not* the mutualistic unrelated partners within the pair, but all of the relatives (offspring, grand-offspring) located in future generations and whose fitness is affected by the initial “switch” to selfishness. The difference with more familiar cases of kin selection is just that, in Fletcher and Doebeli's thought experiment, the causal chain of indirect benefits leading from the actor to the recipients is somewhat less usual—for the mutant

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<sup>13</sup> Mutating into an  $ab$  individual is not the only possible way to induce a switch to selfishness. Indeed, one could as well think of a  $c$  allele which, when present in either an  $Ab$  or  $aB$  individual at either locus ( $Ac$  or  $cB$ ), would produce a selfish phenotype. But in this specific case, the structure of the whole game would be disrupted, as selfishness would now become the dominant strategy. So, because all things must remain equal, the first option must be preferred.

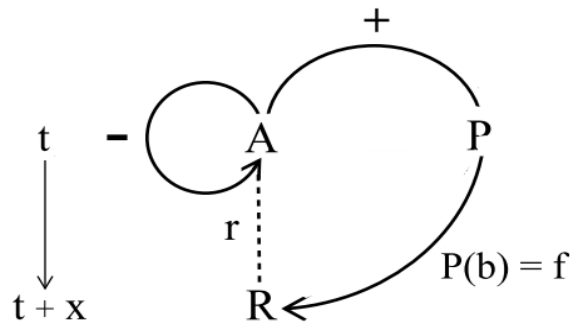
(ab) has to assume the causal responsibility for the harm inflicted to its clonal descendants (a poor reproductive fate). So here is, I think, the true lesson from these authors' thought experiment: even if behaving as an altruist provides no indirect benefits to any individual living in the same generation, it can nevertheless pay *even after the death* of the actor as a form of "inclusive investment", i.e. provided that there are some sufficient guaranties that in the future generations, the consequences of such sacrifice will ultimately benefit its relatives (Lehmann 2008).

Coming back to the cases of mutualistic interactions, I would now illustrate more precisely how this kind of strong altruism can evolve within a symbiotic association. To this end, I will focus on the case of host-symbiont relationships, where the life-span of the host typically exceeds that of the symbionts.

In many host-symbiont associations, strong correlations exist both at the genotypic level and at the phenotypic level. At the genotypic level, symbiont dispersal tends to be limited within the host, which generates a positive relatedness within each subpopulation of host's symbionts (genotypic correlations among symbionts can also be enforced by the host through mechanisms of vertical transmission). At the phenotypic level, altruistic symbionts are associated with the most reactive hosts; and partner fidelity feedback ensures that the benefits of altruistic investments return—in average—to the symbionts' relatives. When both limited dispersal and partner fidelity feedback are sufficiently strong, the cost of altruistic investments tends to be offset by the benefits received by close relatives living in the same host (either now or in later generations); and this synergy, in turn, explains why strong altruism can evolve between the symbionts and their host (Wyatt *et al.* 2013).

This pattern of "inclusive investment" is represented by the following causal diagram (Figure 1).





**Figure 1.** Interspecific altruism (see text for explanation).

In this diagram, A denotes the focal altruistic symbiont, P the host partner, and R the set of recipient symbionts that will benefit from the altruist's contribution either at time  $t$  (the current generation of the altruist) or at time  $t + x$  (the symbionts located at  $x$  generations of the altruist, with  $x \geq 0$ ). The thick arrows represent the causal effects of individual phenotypes on the fitness of P and R, respectively, whereas the dotted line represent the genetic correlation between the focal altruist and the recipients.

As one can see, there are two crucial factors here (represented by  $r$  and  $f$ ) on which the evolution of interspecific altruism relies. The first is the existence of a sufficient amount  $r$  of genetic correlations between the focal altruist and those recipients that indirectly benefit from its initial investment. Thus, if there is an insufficient amount of genetic correlations—e.g. because of a high rate of turnover among the symbiotic strains due to frequent horizontal transmission—the symbionts won't be positively selected to invest in the metabolic activities of the whole association. The second is the partner fidelity feedback (Foster and Wenseleers 2006), measured by the coefficient  $f$ , which denotes the probability  $P(b)$  that an initial altruistic act on the side of A will be repaid (to an amount  $b$ ) by the host to the members of R .

In general, there are two (non-exclusive) ways for the host to provide such a feedback to the symbionts, namely passive and active. With the passive way, symbionts simply invest in the metabolic activities of the host and increase its survival, thus providing a better growing

environment for their relatives within the host. From the symbiont perspective, this can be compared to an altruistic instance of niche construction (Lehmann 2007), but within an organic environment. With the active way, the host adjusts its feedback response to the degree of altruism manifested by its symbionts, e.g. by triggering the production of specific nutrients/chemical compounds, or by regulating its level of immune response. Usually, partner fidelity feedback is more important when the host has evolved mechanisms for responding distinctively to the level of investment of its symbionts; but both passive and active mechanisms can combine to promote the evolution of altruism within a symbiotic association.

In the end, when  $r$ ,  $f$  and  $b$  are sufficiently high to compensate for the cost of the initial investment ( $-c$ ), strong altruism will be favoured by natural (kin) selection within the subpopulations of symbionts—which, having partly renounced to their own reproductive potential, start behaving as *parts* of a broader reproductive unit (the host-symbiont association). Note, however, that such interspecific altruism is expected to be observed less often than intraspecific altruism, for it doesn't only depend on the degree of relatedness among the initial altruist and the ultimate recipients, but also on the probability  $P(b)$  that an initial altruistic act will be effectively “converted” by the partner into benefits ( $b$ ) for the ultimate recipients (indeed, when the benefits altruistic behaviours are mediated by a host partner, the dilution of these benefits does not only occur through  $r$ , but also through  $f$ ).

A final comment must be made on the very use of the term of “interspecific altruism” here. Up to now, I have described the relationship between  $A$  and  $P$  as an instance of strong altruism. However, some might object that, in order for a trait to be considered as altruistic, the ultimate beneficiaries should belong to the same species—which is obviously *not* the case here ( $R \neq P$ ). So, perhaps, the problem of heterogeneity reoccurs in this example?

At first, one could retort that this objection confuses the *conditions* under which altruism can evolve in biological populations with the very *nature* of altruism. But I do believe, for my

part, that the two are related: thus, a trait that could only evolve via direct benefits would *not* properly be regarded as altruistic. However, I think by contrast that the very notion of “ultimate beneficiary” is somewhat misleading here, for it seems to suggest that the benefits provided to R are somehow *more important* than the benefits provided to P. Yet, this is clearly not the case, as the benefits provided to P are *as necessary* to the evolution of the trait as the benefits provided by P to R—indeed, no one (of P and R) is more important than the other (i.e. more “responsible”) in the process driving the evolution of strong altruism here. So, *as long as* the partner is a necessary part of the chain, I would say that the use of the term is fully justified.

## **5. The emergence of a collective heritability at the symbiotic level**

The evolution of interspecific altruism—together with the evolution of a unitary development—constitutes a necessary condition for natural selection to act at the symbiotic level. Yet, in order for interspecific altruism (Fig. 1) to be protected from subversion, specific mechanisms of control must evolve at the symbiotic level. Otherwise, any altruistic participation to the metabolic activities of the whole would remain vulnerable to exploitation by selfish strains of particles; and this, in turn, would prevent symbiotic heritability (i.e. heritable differences in W2) from being decoupled from selection at the lower level.

A first step in this direction is the constitution of a *symbiotic germ line*, which results from the imposition of a vertical mode of transmission of the symbionts. Vertical transmission, as we have seen, ensures a high fidelity feedback between the host and its symbionts, thus increasing, *ceteris paribus*, the common fate between the two partners. But remarkably, this mode of transmission also establishes a kind of division (without any functional specialization, however) analogous to the soma/germen division of reproductive labour of multicellular organisms.

Most of the time, this division concurs with the decoupling between W1 and W2 at the level of the whole symbiotic association, and occurs through the sampling of a few symbionts that are transmitted to the next generation. But this sampling process does not suffice *per se* to preserve the W2 of the associations from being subverted over the long-term. Indeed, an unprotected symbiotic germ line could still be infected or manipulated by selfish strains of microbes (if nothing prevent this to happen). That is why only those associations that have evolved dedicated mechanisms to *protect* the symbiotic germ line from this kind of subversion are likely to evolve higher level adaptations.

What are the mechanisms usually involved in this process? In the evolutionary literature, two kinds of mechanisms are often mentioned, namely (i) an early segregation of the germ line in development and (ii) an immune system (together with the process of apoptosis). Originally, both of these mechanisms have been invoked to explain the evolution of multicellular, clonal organisms (Michod 2000). However, both are also relevant to explain some essential features of highly evolved symbioses. Thus, an early germ line segregation has surely helped to secure the endosymbiosis between plastids/mitochondria and multicellular organisms (Frank 1996),<sup>14</sup> while immune defences have certainly been very efficient at preventing the heritability of many symbiotic characters from being subverted by lower level selection.

To illustrate the role of these mechanisms (in the decoupling between symbiotic heritability and lower level selection), I will focus on two examples that might be related to a form of immune defence. The first is a cellular barrier in the transmission of the symbiont *Buchnera* from bacteriocytes to aphid's embryos. The second concerns the protection of fungi samples (the "symbiotic germ line") in the symbiosis between *Macrotermes* and *Termitomyces*. This latter example, I shall argue, constitutes an interesting illustration of what could be envisaged as a symbiotic "superorganism"—namely a collective composed of several multicellular

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<sup>14</sup> There are some well-known exceptions, like the case of cytoplasmic sterility.

entities who belong to different species and who yet behave, as a whole, like a genuine Darwinian individual.

### **5.1 The aphid-*Buchnera* endosymbiosis.**

In the well-known aphid-*Buchnera* association, both partners are engaged in an obligate relationship (Buchner 1965). The *Buchnera* symbionts are housed in specialized cells located near the aphid's embryos (the "bacteriocytes"), and produce several key nutrients that the host cannot produce itself. The aphid hosts, on the other hand, manage every aspect of *Buchnera* reproduction, and ensure their vertical transmission from one generation to the next.

During the transmission phase, the symbionts are moved from the bacteriocytes to the host's embryos through a coordinated series of exocytotic and endocytotic processes (Koga *et al.* 2012). This guarantees a high partner fidelity feedback between the partners, but also the formation of a symbiotic germ line, as only a few *Buchnera* are transferred to the blastulae in the sampling process. Thus, both conditions 1 and 2 associated with Darwinian individuality are satisfied by this association (cf. section 3).

*Buchnera*, however, is not the only symbiont hosted by *A. pisum*. Indeed, the aphids of this genus often host a facultative symbiont of the genus *Serratia*, which is *not* housed nor present in the bacteriocytes, but nearby—in adjacent cellular structures called the secondary bacteriocytes, as well as in the surrounding hemolymph near the aphid's embryos. Like the *Buchnera* symbionts, *Serratia* are transmitted vertically, and appear to have "coopted" the mechanism of endocytosis used by the former to find their way into the aphid's embryos. Yet, unlike *Buchnera*, *Serratia* is not an obligate symbiont of the aphids—only a conditionally beneficial partner, depending on the ecological context.

In nature, two strains of *A. pisum* coexist, i.e. a disymbiotic strain, with both *Serratia* and *Buchnera*, and a monosymbiotic strain, with *Buchnera* only. When all the *Buchnera* symbionts of the disymbiotic strain are artificially removed from the aphids of the disymbiotic strain, the aphids can still manage to survive, but manifest severe deficiencies (retarded growth, small body size, reduced fecundity). So, from the aphid's perspective, *Serratia* is a less cooperative partner than *Buchnera*, and is better envisaged as a "free-rider".

This "free-rider" character of *Serratia* has been recently corroborated by a study conducted by Koga *et al.* (2012) on the monosymbiotic strain of aphids. In an ingenious experiment, Koga *et al.* artificially infected the monosymbiotic aphids with strains of *Serratia* symbionts obtained from the disymbiotic aphids. Following the injection, the authors observed that *Serratia* was "massively proliferating in hemolymph, often invading primary bacteriocytes, and coexisting with *Buchnera* therein" (p.1231). But they also observed, interestingly, that none of the *Serratia* symbionts who managed to invade the primary bacteriocytes were transferred to the aphid's blastulae through the exocytosis mechanism. Instead, all of the *Serratia* symbionts present in the maternal bacteriocytes remained "stuck" within the body of their new host.

According to these authors, this failure of the *Serratia* symbionts to escape their new host could be due to a selective mechanism that operates at the cellular barrier (ensuring the de-Darwinization of the lower level population of symbionts). The particular details of this mechanism are unknown, but it could have evolved as a way of preventing possible free-riders from invading the symbiotic germ line. Also, it is likely that this mechanism involve cell recognition patterns responsible for the immune protection of the host.

Arguably, the existence of such a cellular barrier would be a good reason for envisaging the whole *Buchnera*-aphid association as a single Darwinian individual. But even so, it should not be conflated with the three-part association aphid-*Serratia*-*Buchnera*. For while the latter constitutes, without doubt, a physiological unit based on multiple, entangled metabolic

processes, its status with respect to the evolutionary ontology is less certain—indeed, there is probably two Darwinian individuals there and not one, i.e. the *Serratia* symbionts on the one hand, and the *Buchnera*/aphid team on the other hand.

## 5.2 The *Macrotermes*-*Termitomyces* symbiosis

The symbiosis between the termites of the genus *Macrotermes* and their fungal partner of the genus *Termitomyces* provides another interesting example of the decoupling between symbiotic heritability and lower level selection. In this well-documented association, the macrotermitines cultivate the fungi into dedicated “fungus comb”—located below their huge nest mound—and feed on the tiny appendices (“nodules”) which are produced by the fungi. In most species of *macrotermitines*, the *Termitomyces* are not inherited vertically from the parental colony, but are acquired “de novo” by the first foraging workers (who find the wind-dispersed spores in the nest environment).

The termites have no interest in the sexual reproduction of their partner, for they cannot eat the costly mushrooms that are produced by the fungi (Korb & Aanen 2003). But there are a few species in which the transmission of the fungal spores is always vertical, including *Macrotermes bellicosus* as well as all known species of *Microtermes*. In *M. bellicosus*, the fungal spores are inoculated to the new colonies by the males; while in all species of *Microtermes*, the fungal spores are transmitted through the females. So, at least in these two cases, something close to a germ/soma separation exists between, on the one hand, the symbionts that altruistically “devote” to the digestion of the cellulose and, on the other hand, the symbionts that are sampled to produce a symbiotic germ line (both conditions 1 and 2 described in section 3 are satisfied).

*Termitomyces* are obligate endosymbionts of the *Macrotermes* colonies. But, as in the *Buchnera*/*Serratia* case, they are not the only individuals in competition for the substrate of the

termites. Indeed, other fungi spores (mostly belonging to the genera *Pseudoxylaria* and *Trichoderma*) are systematically found in the gut/combs of the *Macrotermes* termites.

Several experiments (Visser *et al.* 2011) have shown that “a fungus comb removed from the nest will always be taken over by an aggressive fungus, *Xylaria*, which germinates and quickly overwhelms the comb’s population of *Termitomyces*” (Turner 2004, p.339). Hence, the altruistic production of “ready-to-consume” nodules, through the slow digestion of wood, is certainly not the most efficient strategy against selfish strains of fungi. Surprisingly, however, these other fungi competitors are never expressed in active termite colonies, where their spores remain dormant—which suggests the existence of one or several mechanisms of control that prevent those fungal strains of being expressed in the colony (and, in the case of *M. bellicosus*, of being passed through the symbiotic germ line).

Up to now, two mechanisms have been suggested to explain the stability of the *Macrotermes-Termitomyces* symbiosis. The first is the regulation by the termites of the nest atmosphere, which seems to provide ideal conditions for the development of the *Termitomyces* but not for the other fungi. This regulation is achieved by a process known as “stigmergy”—a process through which the termites adjust the structure of the mound surmounting their nest, so as to keep constant the temperature as well as the CO<sub>2</sub> composition of their atmosphere (Turner 2004). The second is a mechanism of immune defense which has been observed in a species of *Macrotermes* (*M. natalensis*), and which involves a strain of *Bacillus* (Um *et al.* 2013).

In their study, Um *et al.* have shown that the termites of the species *M. natalensis* harbour a *Bacillus* strain (both in their gut and in the fungus combs) that selectively inhibits the putatively antagonistic fungi of *Termitomyces* through the production of a single major antibiotic—bacillaene A. For the authors, “[o]bligat gut passage of the substrate prior to incorporation in the fungus comb may aid this, because this mode of substrate incorporation may allow for the selective inhibition of antagonists before entry to the fungus comb.” (p.2). This suggests that



the *Macrotermes-Termitomyces* symbiosis, at least in the case of *M. natalensis*, has evolved a defense mechanism to protect its functional integrity; and this, in turn, could *possibly* justify its assimilation to a kind of symbiotic Darwinian individual (i.e. a symbiotic “superorganism”) composed of three main parts, namely the termites, its fungus cultivar and the *Bacillus* strain.

In the case of *M. natalensis*, this assimilation is complicated by the fact that there is no vertical transmission of the symbionts. But at least, this example show that the realization of Darwinian individuality at higher symbiotic levels is a topics worthy of further attention—though one should expect to observe it less often at these levels than at the lower levels.

## 6. Conclusion

Two questions arise when one considers the ontological status of symbioses in evolutionary theory, namely:

- (i) when does a given symbiosis count as a unit of selection?
- (ii) when does a given symbiosis count as a Darwinian individual?

Though both are often equated in the philosophical literature, it is important to keep them distinct, for the conditions associated with the former are *not* equivalent to the conditions associated with the latter. The first question, as we have seen, raises difficulties associated with the measure of collective fitness (W1 and W2) and collective heritability at the symbiotic level. The second question, on the other hand, involves an apparent paradox related to the very notion of Darwinian individuality, which implies that the parts of the newly emerged individual have somehow “renounced” to their own reproductive success.

In this paper, I have proposed a tentative answer to each of these questions. With respect to (i), I have suggested that W1 was not an appropriate measure of fitness for symbiotic associations,

and that W2 could be used provided there exists parent-offspring lineages at the symbiotic level. With respect to (ii), I have argued that the apparent paradox related to the idea of a symbiotic Darwinian individual can be solved once we realize that (a) strong altruism can actually evolve between members of different species and that (b) the symbiotic germ line—where the indirect benefits of interspecific altruism are ultimately “concentrated”—can be efficiently protected by mechanisms of control at the symbiotic level. This explanation, furthermore, is also consistent with the relative rarity of symbiotic Darwinian individuals in nature.

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