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DEVELOPING A PHILOSOPHICAL FOUNDATION FOR THE STUDY OF THE MICROBIAL SIDE OF SYMBIOSIS

– Adrian Stencel –

Abstract: Symbiotic associations have been studied extensively in recent years, focusing mainly on the potential benefits to the host. However, understanding the role played by microorganisms in the physiology and fitness of the host, an aspect of the subject that had been neglected for a long time, has now become an important goal of symbiotic studies. Among the interesting philosophical questions are the following: how should we study the impact of symbiosis on the fitness of symbiotic microorganisms? What framework should scientists use, and on what philosophical assumptions should such research be based? In other words, when does comparing fitness make sense? In this paper, I develop such a framework, and argue that these requirements comprise: (i) phenotypically similar individuals put in the same (ii) sub-environment and contrast it with another popular approach. Finally, I apply this to the symbiosis between the *Euprymna scolopes* squid and *Vibrio fischeri* bacteria to show how scientists should evaluate the fitness of symbiotic microorganisms.

Keywords: ecosystems, adaptation, selection, population, fitness

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Introduction[1]

The concept of fitness is arguably at the heart of the theory of evolution. If you were to take any paper in evolutionary biology – or even in some distant field – you would read about fitness differences, fitness advantages, etc. For example, in a paper published very recently, it was shown that a microbial community influences the fitness-related traits of a plant, i.e. the common morning glory, *Ipomoea purpurea*.[2] Similarly, Veltsos et al.[3] argued in a recent paper that there was no evidence for the idea that Y-chromosome differentiation affected male fitness in a Swiss population of common frogs. These exam-

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[2] Chaney and Baucom (2020).

[3] Veltsos, Rodrigues, Studer et al. (2020).

ples suggest that fitness is a key concept in evolutionary biology, since scientists often frame certain results of their research in reference to fitness when they explain them. Accordingly, fitness appears to be a kind of unifying concept. Indeed, it seems that it can be used to study very different biological systems and draw conclusions of the same sort, involving fitness differences. Therefore, it is unsurprising that references to fitness also appear in numerous studies on the microbiomes of multi-cellular organisms.[4]

Microbiome research studies communities of symbiotic microorganisms. These include the microbiomes of certain lakes[5] or soils,[6] but the most interesting research in recent years has focused on the study of microbiomes associated with multi-cellular organisms, aimed primarily at determining the role they play in the evolution and physiology of plants and animals.[7] Furthermore, a great deal of attention has been directed towards understanding how certain symbiotic microorganisms influence the fitness of a multi-cellular host.[8] However, less attention has been dedicated to studying the fitness of symbiotic microorganisms. Garcia and Gerardo[9] argued for a certain design system intended to serve as a framework for the study of the fitness of microorganisms by indicating the settings in which fitness should be compared. The authors mainly argued that in order to understand how symbiosis influences the fitness of symbiotic microorganisms we should compare these microbes in hosts and non-host natural environments. Furthermore, Garcia and Gerardo discussed various potential practical problems connected with this idea. Their framework is important, as it summarises many important studies on symbiosis and suggests how fitness should be measured on that basis.

I oppose their conception in the present paper, intending to show that their framework is based on incorrect philosophical assumptions concerning the commensurability of fitness, and thus ought not to drive research on the fitness of symbiotic microorganisms, although it may prove useful for other types of symbiosis studies. By and large, the comparison of growth in different settings, such as host and non-host media, fails to provide knowledge about fitness differences, and therefore such data should not be used to back up claims concerning the superiority or inferiority (in terms of fitness) of symbiotic vs free-living microorganisms.

The structure of the paper is as follows. Firstly, I will present the concepts of environment and sub-environment. Secondly, I will show which factors must be present in order to compare the fitness of different organisms. I will then argue that the framework of Garcia and Gerardo does not fulfil these requirements. On this basis, I will suggest alternative criteria and present specific biological research in order to implement my framework in actual case studies. Finally, I will present a number of conclusions.

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[4] Suzuki (2017); Gould, Zhang, Lamberti et al. (2018).

[5] Cabello-Yeves, Zemskaya, Zakharenko et al. (2020).

[6] Fierer (2017).

[7] Shreiner, Kao, Young (2015); Rosshart, Vassallo, Angeletti et al. (2017).

[8] Suzuki (2017); Gould, Zhang, Lamberti et al. (2018).

[9] Garcia and Gerardo (2014).

The concept of the environment

The comparison of fitness plays an important role in evolutionary biology as it enables scientists to understand which individuals in a given group are fitter than others.[10] One of the crucial conditions necessary for comparing fitness is the placement of individuals in the same environment.[11] What exactly do we mean when we say they must be placed in the same environment? Colloquially, we can say that certain humans live in the same environment, or that bacteria placed in the same Petri dish live in the same environment, but intuitively we understand that the environment in the former case is much more diverse than in the latter. Therefore, to understand what living in the same environment means, the concept of environment must first be clarified. Some attempts have been made to elaborate upon this concept.[12] In order to show what living in the same environment means, I will rely on the work of Godfrey-Smith[13] and Bourrat:[14] these works appear particularly relevant as both frame this concept within the context of the theory of evolution, to which the concept of fitness is inevitably connected.

I should start by saying that Godfrey-Smith[15] did not explain precisely how he understood the concept of *environment*, even though this word appears from time to time in his book. However, Godfrey-Smith argued that the reproductive output of individuals depends on a combination of properties of two kinds: intrinsic and extrinsic. Although the distinction between them is not free of philosophical problems[16], I will follow it here.[17] What do these two concepts refer to? Generally speaking, on one hand, an individual's intrinsic properties are those that do not depend on the existence of its relationship with other objects. An individual's extrinsic properties, on the other hand, are those that depend in some way on some other object. For example, mass is an intrinsic property of any physical object, whereas weight is an extrinsic property that depends on another object.

In Godfrey-Smith's book,[18] these two concepts, expressed very generally, refer to the "causes" of differences in the reproductive output of individuals. How does this work?

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[10] Comparing fitness can concern types and/or tokens and as well could take place at different levels of the hierarchy of life (cells, individuals, etc.). In this paper, the focus is at the level of individual organisms (specifically microorganisms) and on the fitness of types, because when biologists study the fitness of microorganisms, they usually evaluate the fitness of a given type multiple times in the same environment to gather sufficient statistical data (see Kawecki, Lenski, Ebert et al. 2012; Plech, de Visser, Korona 2014). However, in principle, the framework could be applied to other cases, as Godfrey-Smith's (2009) framework is, in general, very universal.

[11] Brandon (1990); Bourrat (2015a); Abrams (2009); Stencel (2022); Bourrat, Guilhem, Rose et al. (2022).

[12] Brandon (1990); Abrams (2009); Millstein (2014); Bourrat (2015b, 2017).

[13] Godfrey-Smith (2009).

[14] Bourrat (2015b, 2017).

[15] Godfrey-Smith (2009).

[16] For a review, see Marshall and Weatherson (2018) and for a more detailed elaboration Bourrat 2015b, 2017, 2022).

[17] I follow here the early work of Bourrat (2015b, 2017), as I consider it to be more neutral in ontological terms. In 2022, when Bourrat expanded his views on the nature of intrinsic and extrinsic properties, he made ontological claims that I neither endorse nor require for my argument – for instance, the claim that intrinsic vs extrinsic is always a relative distinction, or that everything intrinsic can be said to be extrinsic when viewed from a different perspective and vice versa.

[18] Godfrey-Smith (2009).

Firstly, if intrinsic properties cause reproductive differences, it might be said that we can explain these differences by referring to certain existing variations between individuals. For example, A is characterized by a superior ability to digest and assimilate resources and, as a result, reproduces faster than B. Thus, these differences can be traced back to certain variations between individuals. However, when extrinsic properties come into play, this kind of reference no longer works, because these differences can be traced back not to certain features of the individuals themselves but rather to the different contexts in which they find themselves.

Having presented the fundamental notion, how does the concept of environment fit here? What is an environment in the context of this framework? As Bourrat[19] has pointed out, the distinction between intrinsic and extrinsic properties may be regarded as a way to understand the degree to which individuals inhabit the same environment. According to Bourrat,[20] and also Abrams,[21] an environment is made up of several micro-states. Thus, individuals may find themselves in different micro-states of an environment. For a given entity, each type of micro-state is supposed to lead to different (albeit the same within each type) consequences in terms of reproductive output (which may be highly variable). Thus, what makes one micro-state different from another are differences in extrinsic properties. In other words, if individual 1 is under the influence of extrinsic properties A, B, and C, while individual 2 is under that of extrinsic properties B, C, and D, they inhabit two different micro-states, because their reproductive output is driven by different extrinsic properties. However, they still inhabit the same environment. An organism's environment, therefore, simply comprises all of the potential micro-states weighted by the probability of each state which the organism may inhabit.

I believe that the manner in which Bourrat[22] conceptualized *environment* within the framework of Godfrey-Smith is correct, since it emphasizes that an environment is not homogenous. Rather, as previously noted by many scholars, environments are heterogenous in the majority of cases.[23] In other words, an environment may be characterized by areas that differ from each other (in some way); moreover, organisms may occupy different parts of this environment. This may lead to a number of consequences; for instance, differences in reproductive output may derive from the fact that organisms occupy different parts of the environment. Another reason I believe Bourrat's way of defining *environment* is correct is that he believes environments should be defined with reference to extrinsic properties – indeed, with reference to factors that influence reproductive success, for example, limited access to food in a certain location, or the presence of deadly viruses, toxic substances, etc. This is in agreement with how the concept of environment is often defined; it is frequently understood as a set of environmental factors that have an impact on the survival and reproduction of individuals.[24]

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[19] Bourrat (2015b, 2017).

[20] Bourrat (2015b, 2017).

[21] Abrams (2009).

[22] Bourrat (2015b, 2017).

[23] See Brandon (1990); Abrams (2009); Millstein (2014).

[24] Brandon (1990); Ramsey (2006); Bourrat (2015a); Abrams (2009); Millstein (2014).

This way of defining *environment*, derived from the work of Godfrey-Smith,[25] is thus congruent with the common idea that an environment is heterogenous, but also with another common idea that an environment should consist of the factors that influence the reproductive success of individuals. Therefore, I believe it is justified to define an environment as a collection of all the possible micro-states that individuals can inhabit.

When does comparing fitness make sense?

In the previous section, I introduced two closely related concepts, those of environment and micro-state. Generally, it can be said that the former is just a collection of the latter. This raises the following question: when we compare the fitness of individuals, should we place them in the same environment, in the same micro-state, or in something different? In this section, I will define the concept of a sub-environment and will argue that individuals should be placed in the same sub-environment. Furthermore, I will argue that this view questions the framework suggested by Garcia and Gerardo[26] for research on symbiosis.

Many papers have been published on various aspects of fitness, yet regardless of the concept of fitness employed, the leading aim has always been an understanding of which individuals best fit their environment[27] and thus which are characterized by a higher level of fitness. We can state that those that fare better than others are fitter. Yet this can only be assessed when the environmental background is the same. Consider, for instance, the great diversity of the environments of humans inhabiting the Earth. For instance, if someone from Scandinavia were to fare better than someone in Africa, we would not be very willing to conclude that the Scandinavian is fitter, as the relevant backgrounds are very different. Therefore, it is problematic to treat environment as a point of reference when it is actually heterogeneous; it may transpire that individuals apparently living in the same environment are actually characterized by different extrinsic properties; in other words, they are exposed to different environmental factors. There are two ways of dealing with the problem of defining an individual within its environment. The first is to retain the idea that the environment must be a point of reference. However, this would be problematic, since, as noted by Bourrat,[28] we would have to decide which individuals perform better on average in the face of all potential extrinsic properties found in a given environment, in order to exclude a case in which we compare their fitness when they struggle with different factors – and the number of such cases may be tremendous. Thus, although theoretically possible, this method is troublesome from a practical perspective. The second way is to assume that, in order to compare their fitness, individuals must be compared within a portion of the total environment, that is, within a finite set of micro-states (Fig. 1). Here, I will term such a set

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[25] Godfrey-Smith (2009).

[26] Garcia and Gerardo (2014).

[27] See Brandon (1990); Bouchard and Rosenberg (2004); Matthen and Ariew (2002); Ariew and Lewontin (2004); Ramsey (2006); Abrams (2009); Bouchard (2011); Bourrat (2015a); Stencel (2022).

[28] Bourrat (2015a).

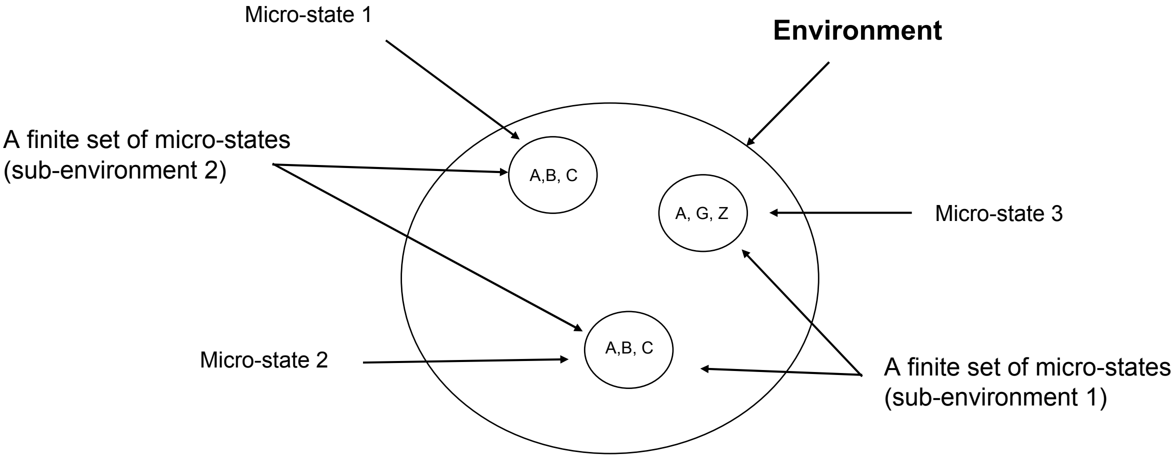

Fig. 1 The figure shows that an environment is composed of all possible micro-states. A sub-environment is a finite set of micro-states. Differences in fitness occur when organisms are placed in the same sub-environment.

a sub-environment and thus when we place individuals in the same sub-environment, they are exposed to the same extrinsic properties. If one individual performs better than another, it would be justified to say that this individual is fitter, as it performs better given the same background conditions. I think the second method is a better choice, as it may be much more useful for practical reasons.

The idea that we should compare the fitness of individuals placed in the same sub-environment is a crucial condition necessary for such a comparison but, as I have noted before,[29] it does not exhaust the list of necessary conditions. Another important condition is the need to compare individuals who are very similar phenotypically. The following thought experiment should help to illuminate this necessity.

We can imagine a world of unlimited resources in which the only extrinsic properties are multiple parasites capable of infecting all species. Some parasites might prosper by using a broad range of hosts and thus this scenario is not hard to imagine.[30] In such a setting, it might transpire that individuals from two different species – e.g. a spider and a cat – will be infected by the same parasites over time, and thus will occupy the same micro-states; therefore, they will inhabit the same sub-environment. If the cat produces more offspring than the spider in such a case, would it be legitimate to conclude that the cat is fitter? I am inclined to say no, because the phenotypes in question differ too much; the life cycles, maximal numbers of offspring, generational timespans, etc., of a spider and a cat are very different, so the fact that one produces more offspring in the same background conditions provides no information about differences in fitness *per se.* The phenotypes in question must be sufficiently similar.

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[29] Stencel (2022).

[30] Combes (2001).

This example, although fictional, shows why it is important to identify the similarity of phenotypes as the second condition.[31] Yet perhaps it would be better to focus on the similarity of intrinsic properties or genetic similarity? I think the former is too abstract for a framework that aims to improve scientific practice. While the latter would be welcome, it potentially excludes cases of convergent evolution,[32] where organisms have phenotypes which might be genetically quite different but they have evolved similar traits because they occupy the same niche. There might be very few cases where this happens; for instance, microbes from different species that live in extreme conditions[33] might be a case due to their very specific environmental conditions. However, such potential cases lead me to believe that phenotype similarity should be considered a second condition.[34]

The idea that we should compare the fitness of phenotypically similar individuals placed in the same sub-environment is in congruence with empirical studies. Scientists studying fitness usually focus on different strains of yeast, bacteria, etc., placed in the same environmental conditions.[35] In the context of the above discussion, it should be clear why this is so. If a fitness comparison is assumed to be an evaluation of which individuals fare better, then individuals must be placed in identical sets of micro-states. A fitness comparison must be limited to phenotype variants put in a given set of sub-environments[36] as they can be exposed to the same extrinsic properties and are sufficiently similar to permit scientists to compare their rates of reproduction.

Returning to the ideas suggested by Garcia and Gerardo,[37] we realize that they are not in congruence with the above suggestions. The authors proposed comparisons of the same phenotype in different sub-environments, for instance, in host vs non-host environments. In the light of everything that has been said in the previous subsections, this does not constitute a correct approach to the study of how symbiosis influences the fitness of symbiotic micro-organisms. Of course, it might still provide interesting information concerning certain things, but it clearly should not be used as a way to study fitness. The following section, relying on the ideas developed in the present paper, suggests which studies are capable of providing knowledge concerning how symbiosis influences the fitness of symbiotic microorganisms.

The Symbiont Side of Symbiosis

A tremendous amount of data is available concerning the influence of microbes on the fitness of hosts,[38] however, as many researchers have noted, we don't really know how being part of a symbiotic system influences the fitness of symbiotic microbes.[39] Further-

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[31] For more arguments, see Stencel (2022).

[32] Futuyma and Kirkpatrick (2017).

[33] Kristjansson and Stetter (1998).

[34] For more see Stencel (2022).

[35] See e.g. Kawecki, Lenski, Ebert et al. (2012); Plech, de Visser and Korona (2014).

[36] Stencel (2022).

[37] Garcia and Gerardo (2014).

[38] Brucker and Bordenstein (2013); Rosshart, Vassallo, Angeletti et al. (2017); Suárez (2018).

[39] Wooldridge (2010); Garcia and Gerardo (2014); Keeling and McCutcheon (2017); Lloyd and Wade (2019).

more, rather than discussing how participation in symbiosis influences the fitness of microbes, scientists tend to use certain metaphors, such as "farming" and "slavery," which are neither informative nor illuminating. Garcia and Gerardo[40] suggested that in order to gain a fuller understanding of symbiotic systems we should focus more closely on evaluating the fitness of symbiotic microbes. This raises a question which is particularly pertinent to this paper: what kind of experiments would inform us about the differences in the fitness of microbial symbionts? Let me briefly summarize one research project before I proceed to answering this question.

The symbiosis between the *Euprymna scolopes* squid and *Vibrio fischeri* bacteria is one of the cases of symbiosis that have been studied in the greatest detail.[41] In this case, it is thought that the host benefits from bacterial bioluminescence, while the bacteria receive metabolic benefits. However, the precise evaluation of the benefits or costs to microbes during such interactions can only be accomplished through well-developed experimental studies.

Wollenberg and Ruby[42] wished to evaluate the actual fitness benefits to bacteria associated with the squid, as well as whether these benefits differed between different strains of *V. fischeri*. These questions stemmed from their previous study,[43] in which they observed that certain strains of *V. fischeri* were overrepresented in the host *E. scolopes* found in Maunalua Bay (MB), Hawaii. In the light organs of the squid, they found a greater abundance of *V. fischeri* strains identified via genetic methods as VfRep-PCR type-I, which, they hypothesized, must be fitter in both host and non-host environmental settings. Therefore, the fundamental idea behind their study[44] was to determine how strains identified as VfRep-PCR type-I (which their phylogenetic analysis identified as a monophyletic group known as Group-A strains) fared in both host and non-host sub-environments, as well as whether it was true that Group-A strains were fitter in both settings, as they hypothesized. For this purpose, they selected several strains from Group A and compared them with non-Group-A strains in different sub-environments. The settings they selected for the experiments comprised inoculated MB bobtail squid and filtered and unfiltered MB seawater.

The above experimental setting is an excellent one, because it also enables us to make a number of interesting comparisons. I will discuss two that are relevant to the present paper. In this experiment we might take, for example, a strain that belongs to Group A and place it in different sub-environment. One day it might be placed in MB unfiltered sea water, another day in the light organ of an MB squid; we could then observe the difference between the placement in these different settings. This was actually one of the comparisons made during the study, showing that Group-A strains grow better in the squid's light organ than in unfiltered MB sea water. But what does this kind of experiment teach us? I think it reveals which sub-environment is more suitable for the growth of a given strain. Indeed, it indicates the sub-environment in which the

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[40] Garcia and Gerardo (2014).

[41] Wollenberg and Ruby (2009, 2012); McFall-Ngai (2014).

[42] Wollenberg and Ruby (2012).

[43] Wollenberg and Ruby (2009).

[44] Wollenberg and Ruby (2012).

phenotype "blossoms" best. However, the issue of differences in fitness is the other way round: we look for the phenotypes that flourish to the greatest extent in a given sub-environment. The study described above also provides the basis for this kind of fitness comparison. We can compare, for example, the growth of a strain from Group A with that of a non-Group-A strain in a MB squid's light organ or in unfiltered MB sea water and see which is better suited to these sub-environments. In fact, this was one of the experiments conducted by the authors of the above study: they compared how strains from both the A and non-A groups fared in unfiltered MB seawater. As it transpired, the latter group fared better. I believe this type of experiment informs us about differences in fitness, because it investigates how different variants of given organisms handle the extrinsic properties presented by a given sub-environment. Indeed, they determine which phenotype variant best fits the sub-environment in question. Therefore, it seems that if we want to understand the differences in fitness between symbiotic microorganisms, we have to compare different strains placed in the same sub-environment.

Do the above experiments fulfil the requirements that I spelled out in the second section and which I think are necessary in order to speak about differences in fitness? These requirements comprise: (i) phenotypically similar individuals put in the same (ii) sub-environment. I believe that this is the case. First of all, I believe we can assume that the individuals were exposed to the same extrinsic properties, because the settings used in the study were designed by those exercising control over those that were included. As a result, I think it is justified to say that when different strains are placed in one given experimental setting (filtered MB water, etc.), they are in the same sub-environment. Secondly, it is necessary to compare the fitness of similar phenotypes. In the experiments above, different strains of *V. fischeri* were used. Since these strains are phenotypically similar, we can assume that, once exposed to the same extrinsic factors, they would be under their influence. Indeed, the similarity of phenotypes between *V. fischeri* strains ensured that they would have to solve the same problems in order to survive and reproduce.

While this sounds promising, it is nevertheless easy to cite differences in fitness in controlled laboratory experiments; it is harder to do so when dealing with organisms living in the wild. We may be able to study their reproductive output, but we can very rarely obtain information about all of the extrinsic properties that may have influenced them. However, I think that the experiment described in this section shows that we can sometimes conduct experiments and extrapolate our results to wild populations. The key here is the reconstruction of a wild micro-state under laboratory conditions. I believe that Wollenberg and Ruby[45] accomplished this quite well in their study, as they made use of natural rather than artificial environments. Accordingly, I believe their conclusions are valid for wild populations – at least to the extent that such conclusions can be valid. The problem is that it is not always possible to use a natural micro-state; indeed, it is not always possible to even culture microbes in the laboratory.[46]

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[45] Ibidem.

[46] See Stewart (2012).

Concluding remarks

The purpose of the present paper was to understand how we should evaluate the influence of symbiosis on the fitness of symbiotic microorganisms. I developed an approach which differs from the one suggested by Garcia and Gerardo.[47] My framework was also supported by reference to those developed by Godfrey-Smith and Bourrat and implemented in certain biological cases. The paper is a continuation and refinement of my previous work[48] as it goes beyond previous case studies, which involved heritable symbiosis, and refines the conditions for fitness commensurability by contextualizing them within the contemporary debate on the concept of environment.

On the meta-level, this paper should be understood as making a contribution to what some consider *philosophy in science*[49] or *philosophy in nature.*[50] The essence of this approach is to "enter" scientific debates, to seek out particular philosophical problems, and to attempt their solution using philosophical tools. The main assumption here is that many scientific debates are problematic due to their enormous philosophical problems.[51] Philosophers, using their philosophical skills, can therefore potentially contribute to these debates. In the present paper, by entering the debate on the microbial side of symbiosis, I have analyzed one example of such a problem (i.e. when does a comparison of fitness make sense?) and also demonstrated how my work might contribute to the planning of future experiments by biologists.

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[47] Garcia and Gerardo (2014).

[48] Stencel (2016, 2022).

[49] Laplane, Mantovani, Adolphs et al. (2019).

[50] Godfrey-Smith (2009).

[51] See Veigl (2017); Veigl, Juárez, Stencel (2022); Nowak and Stencel (2022); Doolittle and Booth (2017); Suárez (2020); Pradeu (2016); Okasha (2018).

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