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Do concepts of individuality account for individuation practices in studies of host-parasite systems? A modelling account of biological individuality

Abstract

In recent discussions the widespread conviction that scientific individuation practices are governed by theories and concepts of biological individuality has been challenged, particularly by advocates of practice-based approaches to individuation and individuality. Some science scholars argue that the function of concepts of individuality is not to provide individuation criteria that guide scientific practice but instead to adequately describe and explain scientific practices. This discussion raises questions about the relationship between individuation practices and concepts of individuality. To explore this relationship, I discuss four scientific studies of host-parasite systems and analyze the respective individuation practices to see whether they correspond to established concepts of biological individuality. My analysis suggests that scientists individuate biological systems on different levels of organization and that the researchers' respective emphasis on one of the levels depends on the research context as well as their epistemic aims and purposes. Thus, it makes sense to use different concepts of individuality to account for different individuation practices. However, not all individuation practices are represented equally well by concepts of biological individuality. The discrepancy between theory and practice results from a reciprocal dependency between concepts of individuality and individuation practices where theory is informed by empirical findings and *vice versa*. To account for this observation, I propose understanding concepts of individuality as abstracted, idealized, or simplified models that only represent certain aspects of scientific practice. A modelling account suggests a pluralistic view of concepts of biological individuality that not only allows the coexistence of different kinds of individuality (e.g. evolutionary individuality, immunological individuality, ecological individuality) but also of normative and descriptive concepts.

Key words: biological individuality, individuation practices, models, pluralism, host-parasite interaction, host-parasite co-evolution

1. Introduction

In discussions of biological individuality, it is often implied that biologists need a clear concept of individuality to successfully carry out empirical work. This conviction is based on at least two assumptions about the relationship between concepts of individuality and scientific practices. The first assumption is

that biologists follow a top-down approach, meaning that they adopt an inner-scientific or meta-scientific[1] concept of individuality and apply this concept to the systems of interest. The second assumption concerns the nature of concepts of individuality. It is believed that concepts of individuality are theories that provide answers to the question "What is an individual?" as well as criteria that enable researchers to determine whether a biological system is an individual or not. In other words, they are understood as prescriptive concepts that govern scientific practices. In this scenario, the role of science scholars would be to construct concepts of individuality that can be used by biologists and guide their practices.

With the rise of practice-oriented approaches to individuation and individuality, however, the priority of the theoretical over the empirical has been challenged (e.g. Kovaka 2015; Nyhardt & Lidgard, 2017; Kendig 2016). Karen Kovaka (2015), for example, characterizes the relationship between concepts of individuality and scientific practices as reciprocally dependent. She argues that empirical research is sensitive to existing concepts of individuality, but scientists do not rigorously follow a top-down approach to individuate biological systems. Others have suggested that science scholars should follow a bottom-up approach and study individuation practices in order to understand for what purposes scientists individuate biological systems and how their practices serve their epistemic aims (Love 2018; Waters 2018). Thus, instead of asking whether concepts of individuality are suitable for guiding scientific practices (e.g. Sterner 2015), one could ask how well these concepts describe and explain scientific practices. The discussion raises interesting questions about the relationship between concepts of individuality and individuation practices. For example, "What exactly is the role of concepts of individuality, to guide empirical work or to describe and explain scientific practices, or both?". But the discussion of the relationship between concepts of individuality and individuation practices also touches on questions about the relationship between scientific practices and concept formation in the sciences and philosophy.

In this article, I explore this relationship by analyzing four studies of host-parasite systems. After describing the scientists' experimental and theoretical work, I focus on the question of how scientists individuate biological systems. As a third step, I analyze to which concepts of individuality these scientific practices[2] correspond and discuss whether the concepts adequately capture the practices in question. I conclude that within one research field, scientists individuate similar biological systems on different levels of organization (e.g. cells, organisms, host-parasite systems as a whole). The researchers' respective emphasis on one of the levels corresponds to their epistemic aims or purposes. Thus, it makes sense to use different concepts of individuality to account for different individuation practices. My analysis also shows that individuation practices of some empirical studies can be captured adequately by concepts of individuality but sometimes there is a mismatch between practice and theory. These findings can be explained by a relationship of reciprocal dependence between meta-scientific and inner-scientific concepts of individuality and individuation practices. Does this mean that the concepts need to be revised, or should scientists rethink and adjust their practices to bring them in line with existing concepts of individuality?

While in some cases one of these two options might be justified, I argue that it is not always required to make adjustments of either theory or practice. Building on Kovaka's (2015) "sensitivity account", I argue that concepts of individuality can be understood as models. Models are not true or false in a general sense, but adequate or inadequate depending on the context of use. Since models of individuality are simplified, abstract, or idealized representations of scientific practice, it cannot be expected that they capture all instances of practice equally well. Instead, concepts of biological individuality are tools that help scientists

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[1] Here, 'inner-scientific' refers to concepts of individuality that are constructed by scientists for the use in science. Meta-scientific concepts of individuality are concepts that are constructed by science scholar (e.g. philosophers and historians of science).

[2] I take the notion of 'scientific practices' to include all types of scientific activities such as experimenting, conceptualizing, explaining and theorizing.

and science scholars understand how and why scientist individuate biological systems and at the same time affect the way scientists and science scholars think about biological entities and processes. Although both theory and practice enter the modelling process, some concepts of biological individuality are located further towards the theoretical pole of the theory-practice continuum while others are more practice-based. This pluralistic approach also allows normative and descriptive concepts to co-exist and maybe even inform each other.

2. Individuation practices

In this section I discuss individuation practices in recent studies of host-parasite systems by means of case studies. Host-parasite systems comprise members of at least two different species that interact in various ways. The question of how researchers individuate biological entities when they study host-parasite systems is particularly interesting because hosts and parasites are often tightly interconnected. In this context I understand 'individuation practices' as the practices that scientists employ to single out a biological system as a distinct entity (see Lowe cited in Bueno et al. 2018, p. 2). In this article I focus on studies of helminths (various species of parasitic worms) and their vertebrate hosts (e.g. fishes, mammals). I discuss scientific practices, particularly experimental research and conceptual practices, e.g. the use and construction of concepts[3]. All four studies are comparable with respect to the organisms that were investigated and to the researchers' engagement with immunology. I first describe each study and subsequently analyze the respective individuation practices and reconstruct these practices by using meta-scientific concepts of biological individuality. For each study I focus on the main unit of analysis identified by the researchers.

2.1. Host-parasite interaction

2.1.1 Description of the study

The first study was published by Jörn Scharsack and his collaborators in 2004 (Scharsack et al. 2004). In their study, the researchers investigated cellular immune responses of three-spined sticklebacks (*Gasterosteus aculeatus*) to infections with tapeworms (*Schistocephalus solidus*). As part of a series of experiments the group infected the fish with tapeworms through ingestion of infected copepods. Since white blood cells indicate an immune reaction to parasites and infections in general, the researchers isolated the sticklebacks' white blood cells and analyzed them using flow cytometry[4]. They also measured the parasites' body weight throughout the observation period of 98 days.

The team found that some of the infected fish had cleared the infection, but others were not able to get rid of the parasite. The analysis of the white blood cells showed that during the initial phase of the infection proportions of granulocytes increased while proportions of lymphocytes[5] decreased. This result is not surprising since the "mobilisation of granulocytes is a common feature of the immune responses of fishes to helminth parasites" (Scharsack et al. 2004, p. 147). However, after day 63 of the infection the proportions of granulocytes decreased while the parasites' body weight increased continuously throughout the observation period. The researchers thus hypothesize that "this might reflect the ability of *S. solidus* to impair the cellular response of its host" (Scharsack et al. 2004, p. 147). Based on their results, Scharsack and his collaborators (2004, p. 148) conclude that the stickleback's immune response is only

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[3] Here, I am not referring to concepts of biological individuality, but to lower-level concepts such as 'organism', 'extended phenotype' (see section 2.2) and 'multibiome' (see section 2.3) that are used as tools to individuate biological systems.
[4] Flow cytometry is a technique that scientists apply to determine the characteristics of cells (e.g. size, surface structure).
[5] Granulocytes and lymphocytes are specific types of white blood cells.

effective against the tapeworm until the parasite has researched a certain developmental stage: "The initial phase of infection seems to be decisive for the development of a parasitosis. It is likely that mobilization and activation of granulocytes can be effective against procercoid[6] stages of *S. solidus* during the first weeks of infection, but once plerocercoid[7] stages are present in the body cavity, granulocytes are unable to develop their activity against *S. solidus.*"

2.1.2 Analysis of individuation practices

For their experiments the scientists use white blood cells to study the stickleback's cellular immune response. Both the research question and the experimental setting presuppose the notion of stickleback and tapeworm as individual organisms with an antagonistic relationship expressed by the concepts of host and parasite. The individuation on the level of the organism precedes the isolation of cells and is at the same time confirmed by the results of the experiment. The focus of this study is on the host and its reaction to the infection with the tapeworm. The scientists conceptualize the white blood cells as belonging the stickleback's immune system that reacts to the parasite by mobilizing granulocytes.

The individuation of cells and organisms in this experiment corresponds to the concept of immunological individuality (Pradeu 2012). Immunological individuality is a kind of physiological individuality that applies immunogenicity, i.e. the ability to induce immune responses, as a criterion for individuality. To put it simply, if an entity is rejected by an organism's immune system, it is not part of that organism (Pradeu 2012, p. 240). Immunological individuality is a boundary-centered approach where the boundaries are established by an organism's immune system. To determine whether or not an entity is part of an organism thus requires knowledge of the organisms' immune responses, e.g. through isolation and analysis of cells. In the article published by Scharsack et al. (2004), the mobilization and activation of granulocytes is clearly interpreted as an immune reaction of the host to an invader. Since tapeworms trigger immune responses in sticklebacks, they are not a part of the stickleback, but separate individuals. Following Pradeu's concept of immunological individuality, one could say that the boundaries between stickleback and tapeworm are established by the stickleback's immune response. Although stickleback and tapeworm were already recognized as individual organisms prior to the experiment, the immunological individuality of the stickleback was confirmed by the analysis of its white blood cells.

2.2. How host evolution affects parasites

2.2.1 Description of the study

The second case study is an experiment conducted by Jesse Weber and his team (2017) who have also conducted research on the stickleback-tapeworm experimental system. The starting point of the study was the observation that populations of sticklebacks (*Gasterosteus aculeatus*) on Vancouver Island varied significantly in their infection prevalence.[8] The Gosling Lake (GOS) population, for example, exhibited an infection prevalence of 50-80% while no tapeworm (Schistocephalus solidus) infections were observed in the Roberts Lake (ROB) population. The aim of the group's research was to test whether these two populations vary with respect to immune phenotypes and to evaluate whether there are underlying genetic differences that explain the variation (Weber et al. 2017). To see whether the variations in infection prevalence is associated with heritable differences in immune response, the team conducted a

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[6] The procercoid stage is the first larval stage of the tapeworm.
[7] The plerocercoid stage is the second larval stage of the tapeworm.
[8] Sticklebacks in 50 Lakes on Vancouver Island were monitored over a time period of 10 years (Weber et al., 2017).

breeding experiment in the laboratory. Wild-caught stickleback from GOS and ROB were bred and crossed to generate different pure and hybrid populations (Weber et al. 2017, p. 6576).

As in the experiment discussed in section 2.1., the fish were fed infected copepods and the infection frequency (proportion of stickleback with *S. solidus*), infection intensity (abundance of *S. solidus* per fish), and mass of the tapeworms were measured. Interestingly, GOS and ROB stickleback did not differ significantly in the frequency or intensity of laboratory infections, however, the parasites grew dramatically larger in GOS than in ROB stickleback. On average, the mass of tapeworms isolated from GOS stickleback was 34-fold larger than the mass of tapeworms from ROB stickleback. In the hybrid populations (GOS stickleback crossed with ROB stickleback) the tapeworms grew to intermediate size (Weber et al. 2017, p. 6577). According to Weber et al. (2017, p. 6577) "these results demonstrate [that] there are heritable and thus evolved differences between the ROB and GOS stickleback, given differences in laboratory-raised sticklebacks' ability to suppress tapeworm growth. The intermediate size of parasites in hybrid fish also strongly suggests an additive genetic basis for this evolutionary difference". Since growth suppression constrains the tapeworms' reproductive potential, the greater resistance of ROB stickleback decreases the parasites' fitness (Weber et al. 2007, p. 6577). Weber et al. (2017) argue that "this measure of parasite success represents an extended phenotype of the stickleback, in the sense that the host's genotype alters the parasite's phenotype" (p. 6577).

2.2.2 Analysis of individuation practices

Like the case discussed in the previous section, individuation takes place both prior to the experiment and in the course of evaluating and explaining the results. The way in which Weber et al. (2017) describe the starting point of the experiment and the experimental design shows that the stickleback and the tapeworm are individuated both on the level of the organisms and on the population level. The individuated organisms represent their respective populations (ROB and GOS stickleback). Host and parasite, however, do not evolve completely separately, but their evolutionary trajectories are intertwined (Weber et al. 2017, p. 6575).Thus, the parasite is not only seen as the host's immunological antagonist but also as its evolutionary antagonist in the sense that parasite adaptation to the host is followed by host adaptation and so on. This evolutionary scenario where adaptations are followed by counter-adaptations of the opposing species is also known as Red Queen hypothesis [9] (van Valen 1973).

To explain their experimental results, Weber et al. (2017) draw on the concept of the extended phenotype that was introduced by Richard Dawkins (1999). The concept of the extended phenotype is closely linked to his concept of the selfish gene. He favors a gene-centered of evolution and understands the gene as the central unit of selection (Dawkins 1976). He argues that the concept of phenotype should be extended to include "all effects of genes upon the world" (e.g. on the cell, the organisms' body, artefacts such as spider webs) (Dawkins 1999, p. 293). In the discussion of the experiment conducted by Weber and his collaborators (2017), the parasite's growth is considered belonging to the extended phenotype of the host. Following Dawkins, this would mean that the small size of tapeworms from ROB stickleback is an effect of ROB stickleback genes. Weber et al. (2017) only examined whether there is an underlying genetic difference between ROB and GOS stickleback. However, they did not study what exactly the genetic differences are and therefore the genes responsible for the repression of tapeworm growth have not been individuated.

In the experiment the focus is not on the nature of the immunological reaction itself but on the evolutionary interconnectedness of host and parasite. Therefore, I explore whether the explanatory

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[9] The name of the hypothesis is derived from Lewis Carroll's novel *Through the Looking-Glass and What Alice found There*. In the novel, the Red Queen says to Alice, "Now, here, you see, it takes all the running you can do, to keep in the same place".

practices in question can be reconstructed by using concepts of evolutionary individuality. In the literature, evolutionary individuality is usually associated with units of selection (e.g. Lewontin 1970; Gould and Lloyd 1999; Godfrey-Smith 2009). I have shown that Weber and his collaborators view the stickleback and the tapeworm as evolutionarily intertwined. The question is thus whether the host-parasite system as described by Weber et al. (2017) can be characterized as an evolutionary individual. I argue that this is not the case because the host-parasite system as a whole is not targeted by selection and the host's fitness is not aligned with the parasite's fitness (Clarke, 2013; Bourrat & Griffiths, 2018). It has been argued that multispecies conglomerates can be considered evolutionary individuals. Ereshefsky and Pedroso (2015), for example, claim that multispecies biofilms could be considered evolutionary individuals on the basis of certain characteristics such as internal integrity, division of labor, coordination among parts, and heritable adaptive traits. In Weber et al.'s study, the host and the parasite are described as evolutionary antagonists, meaning that an adaptation that benefits the stickleback (e.g. growth suppression of the parasite) decreases the tapeworm's fitness. The adaptation in question is therefore not situated on the level of the host-parasite system as a whole. Although the stickleback-tapeworm system exhibits a certain degree of integrity, there is no division of labor or coordination among parts. Therefore, the system fails to meet at least three of the four criteria suggested by Ereshefsky and Pedroso (2015). On that basis, it seems plausible to argue that the stickleback-tapeworm system as described by Weber and his team is not a unit of selection because host and parasite are conceptualized as antagonists that are not "ultimately 'in the same boat'" (Bourrat & Griffiths, 2018, p. 33).

To simply reconstruct the researchers' individuation practices in terms of physiological individuality (stickleback and tapeworm as individual organisms), however, would not adequately capture the close causal relationship between the evolutionary trajectories of stickleback and tapeworm expressed by the use of the concept 'extended phenotype' and the description of Red Queen dynamics. Concepts of species or lineages as individuals (e.g. Ghiselin 1974; Hull 1978) could account for the individuation of organisms as representatives of a population, but do not account for the evolutionary interconnectedness of host and parasite. To my knowledge, there is no established meta-scientific concept of biological individuality that accounts for the conceptualization of parasite size as a phenotypic expression of host genes. One could therefore conclude that there is a need for a new concept of biological individuality that accounts for the close-knit evolutionary trajectories of hosts and parasites as well as their antagonistic relationship that does not amount to adaptive traits on the level of the host-parasite system as a whole. Another approach would be to recommend the scientists to rethink their use of the concept of the extended phenotype in this context and find a different way of explaining their results.

2.3. The intestinal ecosystem

2.3.1 Description of the study

The article discussed in this section is a review by Heather Filyk and Lisa Osborne published in 2016. In their article they introduce the concept of the multibiome and review literature on multibiome-host interactions and interactions between members of the multibiome. The term 'multibiome' is introduced "to encompass the diverse collection of microscopic (bacteria, archaea, fungi) and macroscopic (multicellular worms) organisms, as well as viruses […] that colonize mammals" (Filyk & Osborne 2016, p. 47). The multibiome is comprised of four subsystems, the bacterial microbiome, the virome, the mycobiome and the macrobiome. The authors discuss the respective systems separately but also highlight the interactions between subsystems and with the host. According to Filyk and Osborne helminths belong to the microbiome. In the article, the authors discuss several interactions that involve helminths. The reviewed literature suggests, for example, that helminths alter the composition of the bacterial microbiome which can directly influence the host's immune homeostasis and responses to pathogens

(Filyk and Osborne 2016, p. 49). Helminth-induced immunomodulation can also impair antiviral immunity to newly acquired intestinal viral infection (Filyk and Osborne 2016, p. 50). Helminths also use commensal bacteria as cues that they have reached their destination to develop (Filyk and Osborne 2016, p. 49).

2.3.2 Analysis of individuation practices

Filyk and Osborne (2016) emphasize the interactions between intestinal entities and understand the multibiome as an ecosystem that is regulated by these interactions: "Similar to other ecosystems, the intestinal community is dynamic, responsive, and regulated by interactions between distinct biological entities" (p. 49). To present the results of their literature review, the authors individuate nested biological systems, e.g. host organism, the entire intestinal ecosystem (multibiome) and subsystems comprised of members of several species such as the macrobiome and the bacterial microbiome. In this study helminths are conceptualized as constituents of an ecosystem and the host is conceptualized as the environment of the multibiome with which interactions take place. Since the multibiome is the central concept in Filyk and Osborne's article, I will focus my discussion on this concept.

The previously discussed concepts of biological individuality do not account for the individuation practices of this study. Since the multibiome as a whole does not have an immune system, the concept of immunological individuality does not apply. Under a concept of evolutionary individuality, the multibiome or other communities would not be considered an individual because it is not targeted by selection (see Huneman 2014b). The individuation of ecosystems like the multibiome, however, corresponds to Philippe Huneman's (2014a, 2014b) "weak concept of individuality". The concept is based on the notion of quasi-independence. In a quasi-independent subsystem, the interactions between elements in the system are stronger than interactions between external elements (Huneman 2014a, p. 364). The weak concept of individuality prioritizes interactions over boundaries and is therefore a concept of ecological individuality. Since the application of the concept produces nested individuals (Huneman, 2014b), it corresponds well to Filyk and Osborne's approach to individuation of nested biological systems. It is, however, a formal concept and its application to a system requires a theory to define the variables in question and empirically determine individuality. It can therefore be applied to different types of systems (e.g. cells, organisms, communities) by choosing a relevant theory (Huneman 2014b). The question of whether the multibiome is an individual is thus an empirical question that cannot be answered on the basis of the information provided by the authors of the review. However, Huneman (2014b, p. 376) states that both the host organism and the gut microbiome are individuals under his weak concept of individuality. It is unclear whether his notion of 'gut microbiome' also comprises helminths, but with the information in the article by Filyk and Osborne, it is plausible to argue that the multibiome exhibits a higher degree of individuality than a randomly assembled set of organisms and that the individuation of this system based on interactions among members of the system is non-arbitrary. An advantage of Huneman's concept is that the strength of interactions between elements of a systems is independent of the question whether an entity is a living being or not. Viruses could therefore also be included in the analysis of the system's individuality without the need to discuss their ontological status.

2.4. Helminths as old friends

2.4.1 Description of the study

Like the individuation practices discussed in the previous section, the following case is an instance of individuation in the context of scientific theorizing, not experimental individuation. In this section I discuss several articles by Graham Rook (2009, 2010, 2012) on a similar topic, the so-called old-friends hypothesis.

Rook (2010, 2012) explicitly locates the old-friends hypothesis in the context of Darwinian Medicine, an approach that applies evolutionary theory to medical problems. Darwinian Medicine is a framework that uses adaptationism as a heuristic principle to explain human health and disease. Proponents of Darwinian Medicine assume that humans are genetically adapted to the hunter-gatherer environment of the Palaeolithic and maladapted to modern environments of the industrialized Global North (mismatch hypothesis) which makes them susceptible to certain diseases (Méthot 2011, p. 78). Rook applies these theoretical principles and discusses immunological studies of host-parasite interaction. His aim is to show that and explain why the absence of helminths (and other organisms) plays an important role in the development of chronic inflammatory disorders in humans.

Rook (2010, p. 74) argues that helminths and other organisms "have been present, inevitably and continuously, from relatively early in the evolution of the immune system" and came to play an important role in immune regulation through a process of host-parasite coevolution. Due to their long association with humans, some species have evolved into commensals (i.e., old friends) (Rook 2009). Rook (2010) argues that the human immune system is not able to get rid of helminths and over time it came to depend on the presence of these organisms: "If we are thinking in a Darwinian way, we should be starting from the hypothesis that any organism that has been consistently present for a significant part of mammalian evolution might have been 'written into' the mammalian genome, because 'Evolution turns the inevitable into a necessity'" (p. 70). He takes the argument one step further and claims that the deprivation of certain organisms such as helminths contributes to the development of chronic inflammatory disorders, e.g. autoimmunity (Rook 2010, 2012). According to Rook the proper functioning of our immune system depends on the presence of these organisms who have evolved from parasites into "friends" and "partners". This so-called evolved dependence "refers to situations where an organism has become adapted to the presence of a partner through loss of genetic material, and can no longer function without that partner" (Rook 2010, p. 71). The old-friends hypothesis would explain, for example, why autoimmune diseases are more common in Europe and North America than in countries of the Global South where helminth infections are prevalent (Rook 2012; WHO 2019).

2.4.2 Analysis of individuation practices

In Rook's work helminths are not referred to as 'parasites' and are not seen as invaders or opponents, but as friends and partners. Human-helminth interaction is conceptualized as a symbiotic relationship in which both partners benefit from the alliance. As in the study discussed in section 2.3, Rook's individuation practices result in nested entities. Host and "parasite" are referred to as individual organisms but also a whole. While the focus in the article by Filyk and Osborne (2016) is on the intestinal ecosystem and interactions therein, Rook (2010) sees helminths as an integrated part of the human immune system. Thus, Rook's emphasis is on the functioning of the host-parasite system as a whole. Although Rook does not explicitly use the concept of the holobiont, it would apply to his notion of helminths and other organisms as integrated parts of the human immune system. The term 'holobiont' refers to a functionally, genetically, and spatially integrated biological unit that comprises a host and its symbiotic microbiota[10] (Zilber-Rosenberg & Rosenberg 2008; Moran & Sloan 2015; Theis et al. 2016, Catania et al. 2017).

The question is whether the human-helminth holobiont as described by Rook also corresponds to a concept of biological individuality. Rook's work is related to the study discussed in the previous section. I have argued that the multibiome is an ecological individual under the weak concept of individuality. As I have already mentioned, the concept is versatile and can be applied to many different entities and levels

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[10] In this context, the term 'microbiota' is used broadly and refers to an assemblage of bacteria, archaea, viruses, protists, fungi, and helminths.

of individuality. Since the interactions between holobiont components are stronger than interactions between external components and holobiont, the holobiont is also an ecological individual under Huneman's concept. But do strong concepts of individuality also apply in this case? Although helminths trigger immune responses in humans, Pradeu's concept of immunological individuality would not adequately represent Rook's conception of helminths as integrated parts of the human immune system. According to Rook, however, the helminth-induced immune response is what protects the host against autoimmune diseases and thus the helminth is not the human's immunological antagonist but an integrated part of their immune system. If one were to understand the concept of immunological individuality as prescriptive, however, one could argue that Rook's theorizing is flawed, and helminths should not be conceptualized as an integrated part of the human immune system.

Another possible candidate is evolutionary individuality, especially because Rook emphasizes the evolutionary dynamics that have led to the integration of helminths into the human immune system. As I have already mentioned, evolutionary individuality is usually associated with units of selection. Most authors agree that the holobiont is an entity targeted by natural selection (Godfrey-Smith 2009; Dupré & O'Malley 2009; Ereshefsky & Pedroso 2013, 2015; Godfrey-Smith 2012). Holobionts also exhibit other features associated with evolutionary individuality, e.g. they are integrated wholes, they are more or less delineated from their environments, and they have holobiont-level adaptive traits (Catania et al. 2017). They do not, however, reproduce on the level of the holobiont and they do not always form lineages with vertical transmission (from parents to offspring) of microbiota (Godfrey-Smith 2009, 2013; Booth 2014). Especially in the case of human-helminth systems, helminths do not spend their entire life cycle inside the host but are acquired from the environment. A hookworm (*Necator americanus*) larva, for example, hatches and grows in the soil and is able to penetrate the human skin when it has reached the third larval stage (Hotez et al. 2004). The adult worms lay eggs inside the human intestinal system and leave the body through feces (Howdon and Hotez 1996). Therefore, the parasite is not directly transmitted from parents to offspring. For some authors this point is crucial for characterizing holobionts as ecological communities rather than evolutionary individuals (e.g. Skillings 2016; Bourrat and Griffiths 2018). Others, however, see holobionts as evolutionary individuals although they do not reproduce as a unit. Ereshefsky & Pedroso (2015), for example, argue that instead of denying the holobiont's individuality, we should rethink our concepts of evolutionary individuality. To sum up, the answer to the question whether the holobiont is an evolutionary individual depends of the criteria for evolutionary individuality. If one prioritizes functional integration over vertical transmission, the holobiont could be considered a biological individual in a strong sense.

3. Individuation on different levels

In the previous section I have discussed four studies on helminths and their vertebrate hosts. My analysis suggests a plurality of individuation practices on different levels that correspond to different concepts of individuality and different notions of hosts and parasites. In the first study researchers investigated the cellular immune responses of sticklebacks infected with tapeworms. To this end, Scharsack and his collaborators individuated organisms and host cells. They conceptualized tapeworm and stickleback as individual organisms with an antagonistic relationship. The experiment showed that the tapeworm provoked an immune response in the stickleback. Scharsack et al.'s individuation practices are best captured by an approach that builds upon a physiological concept of individuality, namely immunological individuality. In this case, the stickleback can be understood as an immunological individual and the tapeworm is the invader that the stickleback's immune system is trying to fight off. In the second case, the researchers tested whether two different stickleback populations vary with respect to immune phenotypes and evaluated whether there are underlying genetic differences. In this experimental study stickleback and tapeworm were also conceptualized as antagonists. The scientists found that stickleback

genes have an effect of the tapeworm's phenotype and therefore characterized the helminth as part of an extended phenotype of the host. I have shown that neither physiological nor evolutionary individuality account for the experimental and explanatory practices in question.

The third and fourth case represent individuation practices in scientific theorizing. Filyk and Osborne introduced the concept of the multibiome to account for the diversity of and interactions among biological entities of the mammalian intestinal system. Rook put forward the old-friends hypothesis to explain the prevalence of autoimmune diseases in industrialized countries. In the study discussed in section 2.3, helminths are conceptualized as constituents of the mammalian intestinal ecosystem (the multibiome) while Rook sees them as constituents of a holobiont. Both the multibiome and the holobiont are biological wholes on different levels. Therefore, both can be characterized as ecological individuals by applying the concept of weak individuality. Whether or not the holobiont can additionally be characterized as an evolutionary individual depends on the respective criteria for evolutionary individuality and whether one prioritizes functional integration or vertical transmission of genetic material. In all four studies individuation takes place on different levels which results in nested biological systems. Scharsack et al. (2004), for example, individuate organisms and cells while Filyk and Osborne (2016) individuate the host organism, the multibiome, its subsystems (e.g. macrobiome), and species. I have shown that some of the individuated systems are identical. Helminth and host, for example, are addressed as individual organisms in each of the four studies. Two studies (2.3 and 2.4) additionally individuate the host-parasite system as a whole. My analysis suggests that the partitioning frame, i.e. the criteria for identifying and individuating biological entities (see Winther 2006) seems to be similar in all four studies. In none of the studies the researchers individuated entities like molecules, organs, or genes. This is probably owed to the fact that the respective scientists work in similar fields and share the same theoretical perspective (Winther 2006). However, the scientists' emphasis differs with respect to the levels of organization. Depending on the research question, they concentrate either on individual organisms, populations, systems that comprise members of different species, or the host-parasite system as a whole.

The results of my analysis suggest that individuation practices are, to a certain extent, linked to research fields in the sense that scientists seem to draw from the same repertoire of biological entities even when following different projects within one field. Individuation practices could also depend on the kinds of organisms that are studied by the scientists. The variety of levels of organization and the different concepts of helminths and vertebrate hosts (e.g. helminth as invader vs. friend) and their relationship (host and parasite as individual organisms in an antagonistic relationship vs. helminths as integrated parts of the host's immune system), however, suggests that the kind of organism is not the main factor. Instead, the researchers' focus on a certain level of organization is guided by their research questions (see Love 2018). Thus, the focus on different levels of organization corresponds to different epistemic aims, purposes, and contexts of investigation (Love & Brigandt 2017; Waters 2018; Reydon 2019). These purposes, however, are not adequately captured by general categories such as explaining, predicting, manipulating etc., but are more fine-grained and local (see Waters 2018). For example, in the studies discussed in the previous section, scientist individuated units to explain specific aspects about host-parasite systems. The study by Weber and his collaborators, for example, explains why tapeworms grow larger in one population of sticklebacks than in another population. The old-friends hypothesis, on the other hand, is a possible explanation for the fact that very few people in countries of the Global South suffer from allergies and other autoimmune diseases while these diseases are prevalent in countries of the Global North. Therefore, explanations of different phenomena in similar organisms can require a focus on different levels of organization. It is also important to note that scientist sometimes use different concepts for individuating entities during different stages of their work. Weber and is team, for example, conceptualized stickleback and helminth as individual organisms that represent populations for the purpose of experimentally manipulating and analysing them. For explaining their interaction, however, they used the concept of the extended phenotype.

I have shown that individuation practices do not necessarily map neatly onto established concepts of individuality. Since the weak concept of individuality developed by Huneman is a formal concept that requires a theoretical basis to empirically determine individuality, it is versatile and could potentially be used to account for individuation practices in all four studies. Stronger concepts of individuality like physiological or evolutionary individuality, however, do not apply to at least two of the studies (sections 2.2 and 2.3). In the first study, the concept of immunological individuality captures Scharsack et al.'s individuation practices quite well while there is no established concept of strong biological individuality that adequately captures Weber et al.'s explanatory practices. The studies discussed in section 2 suggest that in some cases theory (concepts of individuality) and practice (individuation) are well matched. However, as we have seen, this is not always the case. These findings and the fact that none of the researchers discuss concepts of individuality in their publications could mean that the scientist consider their concept of individuality to be clear and do not see the need to mention it in the text or they do not necessarily follow a top-down strategy to individuate entities, meaning that their practices are not strictly guided by concepts of individuality (Kovaka 2015). In the following section I will discuss this question and argue that concepts of individuality can be understood as models that do not necessarily represent all instances of scientific practice.

4. Concepts of individuality as models

Although most scientists do not seem to have a clear-cut answer to the question "What entities are biological individuals?", they are able to successfully individuate living systems for their respective purposes (Kovaka 2015). A fundamental theory of individuality is thus unnecessary and maybe even unwarranted for individuation practices (Love 2018, p. 185). Often, scientists use lower-level concepts like 'organism' or 'holobiont' as tools to individuate biological systems (Waters 2018; Catania et al. 2017) and their individuation practices are guided by their research questions (Love 2018) as well as practical considerations. Karen Kovaka (2015) argues against the widespread conviction that individuation practices depend on theories of biological individuality and proposes a "sensitivity account" to characterize the relationship between theory and practice. She argues that "biologists do not need to know what a biological individual is in order to do good empirical work, but which objects they count as individuals does affect their thinking about biological processes" (p. 1095). In turn, empirical findings can influence the way scientists and science scholars think about biological individuality and alter individuation criteria.

Scientific practices are informed by theoretical concepts and *vice versa*; the relationship between concepts of individuality and individuation practices is one of "mutual dependence" (Kovaka 2015, p. 1102). A relationship of mutual dependence explains the fact that established concepts of individuality do not capture the practices discussed in section 2 equally well. A mismatch between the theoretical and the practical can appear because individuation of biological systems is not entirely governed by concepts and theories, nor are concepts of biological individuality entirely based on scientific practices. Similarly, the relationship between inner-scientific and meta-scientific concepts of individuality is one of reciprocal dependence. It is also possible that meta-scientific concepts are strongly influenced by individuation practices and *vice versa*. I thus propose to conceptualize the relationship between theory and practice as a triangle of relationships of reciprocal dependence between individuation practices, inner-scientific concept formation and meta-scientific concept formation (Figure 1).
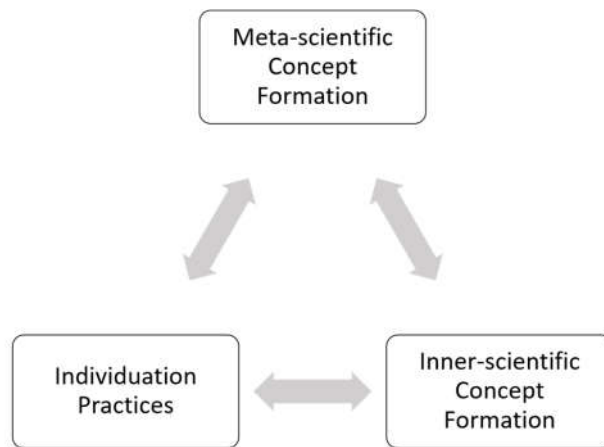
Figure 1: Relationships between individuation practices and concept formation

As I have shown in the previous sections, some individuation practices cannot be adequately captured by established theoretical accounts of biological individuality. Alan Love's (2018) study of individuation practices in developmental biology has yielded similar results. He argues that there is a mismatch between theory and practice because "developmental biologists do not rely on a theory of biological individuality based on natural selection to track developing embryos and their component parts" (p. 185). According to Love (2018) their research is not governed by a fundamental theory, but instead guided by structured problems. Therefore, "the appeal to fundamental theory from evolutionary biology [as in Clarke's (2010, 2013) and Godfrey-Smith's (2009, 2013) accounts of individuality] gets it wrong" (p. 185). He thus suggests that philosophers should focus their attention on individuation practices to generate accounts that describe and explain scientific practices adequately (Love 2018, p. 188). However, Love does not discuss other kinds of concepts of biological individuality (e.g. developmental individuality, physiological individuality) to see if they capture the practices in developmental biology better than concepts of evolutionary individuality.

I agree that a bottom-up approach from individuation practices to meta-scientifc concept formation would yield accounts of biological individuality that are more in line with scientific practice. Pradeu's concept of immunological individuality, for example, resulted from philosophical inquiry that is strongly practice-oriented. My analysis of Scharsack et al's practices shows that Pradeu's insights into scientific practices and collaboration with immunologists yielded a concept of individuality that accounts for certain individuation practices in immunological research. However, his account is rather local and does not capture other practices discussed in section 2. I would not say, however, that Pradeu's appeal to immunological theory gets it wrong in the other cases (e.g. Rook's work on the old-friends hypothesis). Instead, I propose that concepts of individuality can be understood as different models. In this context, models are simplified accounts that help scientists and philosophers to describe, understand, and gain access to biological phenomena (see Bailer-Jones 2002, Morgan 2001). As models, concepts of individuality can be abstract and general (e.g. Huneman's concept of ecological individuality) or specific (e.g. Pradeu's concept of immunological individuality) representations of scientific practice.[11] More specific concepts are local in the sense that they only represent certain aspects of scientific practice or practices revolving around certain research questions, but they include rather concrete individuation criteria (e.g.

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[11] The distinction between specific and general concepts should not be understood as a dichotomy but rather as two poles of a continuum.

immunogenicity). General concepts provide very general individuation criteria (e.g. the strength of interactions) and thus represent a larger class of individuation practices in various fields and contexts.

As models, concepts of individuality are flawed by definition. Models are abstract, idealize, simplify or omit certain aspects of the target phenomena (Morrison & Morgan 1991; Giere 2004; Frigg & Hartmann 2018). Thus, they do not represent all instances of target phenomena equally well. Instead, they are tools (Parker 2010; Knuuttila 2011) for different purposes like manipulation, prediction, or explanation. At the same time, representations like models influence the way we perceive the world (see Winther, 2020).[12] Although concepts of individuality do not perfectly represent scientific practice, they are still useful tools that help science scholars describe and explain scientific practices and at the same time inform the way scientist perceive their research objects. Concepts of biological individuality are not constructed in strict top-down or bottom-up approaches. Instead, they are situated somewhere between theory and practice because both empirical findings and theory enter into the modelling process (Morrison & Morgan, 1991). Understanding concepts of individuality as models is therefore in line with the relationship of reciprocal dependence between theory and practice as described by Kovaka (2015). My analysis of the cases presented in section 2 suggests that similar organisms and systems are conceptualized and individuated differently in different research contexts which suggests a pluralistic view of biological individuality. A modelling account of biological individuality is compatible with a pluralism of different kinds biological individuality such as developmental individuality, evolutionary individuality, physiological individuality (see DiFrisco, 2019). In most cases, it might even be adequate to represent individuation practices with more than one model because the practices are too complex to be represented by only one model of individuality. Considering the diversity of scientific practices and the complexity of biological entities, it seems impossible to capture all aspects of this variety with only one model of biological individuality (see Kovaka 2015). A modelling account of biological individuality also suggests pluralism with respect to the question whether concepts of individuality should be normative or descriptive. While some concepts of individuality adequately describe certain aspects of scientific practice in certain contexts, other concepts of individuality are normative because they guide scientific practices. For example, concepts of evolutionary individuality can guide the choice of evolutionary models or provide a coherent categorization of biological entities (Sterner 2015, p. 614). Concepts of biological individuality can also be normative when they are applied in ethical discussions (e.g. discussions of intrinsic value of or moral obligation towards biological entities; see e.g. Millstein 2018). However, most concepts are probably located somewhere in between the two poles of the descriptive-normative continuum.

With the view of concepts of individuality as models, the question is no longer whether or not the model gets it right or whether it is true, but whether it is adequate for the purposes in question (Parker 2009). Therefore, in the case described by Love (2018) the conclusion would be that concepts of individuality that are based on evolutionary theory are not adequate for representing the individuation practices applied by developmental biologists. This does not necessarily mean that there is something wrong with the model, but maybe only that this particular model is not the right tool for the job. A concept of developmental individuality would probably be more suitable in this case. Of course, models can and should be revised on the basis of empirical findings, but in this case, it seems more appropriate to find a different model or create a new one. Even if suitable models (such as concepts of developmental individuality) already exist, it is unlikely that they represent all aspects of scientific practice perfectly. Thus, my answer to the question 'Do scientists need to adjust their practices to bring them in line with existing concepts or should the concepts of biological individuality be revised?' is 'both and neither'. Depending on the context, it might be appropriate to revise the model while in other cases scientists might want to rethink their practices. If

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[12] Blackwell and Engelhardt (2002) present a similar argument and claim that representations like diagrams affect mental representations of phenomena. The London Underground map, for example, has changed people's "mental map" of distances across London (p. 54).

the model is good enough, however, it may also be justified to use a model that is flawed to a certain degree as long as one is aware of the model's limitations. In the case of the human-helminth holobiont (section 2.4), for example, one could argue that existing concepts of evolutionary individuality account for the practices in question, even though holobionts do not exhibit all features associated with evolutionary individuality.

Acknowledgements

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