PiBM Newsletter

June 2024

Introduction

Hello PiBM network members!

We have quite the newsletter in store for you this month. Alongside the always exciting announcements of post-graduate positions, jobs, and publications, we have thoughtful reports and reflections. First, you will find reports by students on their experiences attending the recent PiBM Summer School in Bordeaux - which we were grateful to receive and happy to share. Then, you will find an insightful reflection by a cherished PiBM member, Kevin Lala, on how philosophy has influenced his work in biology and tastes of a forthcoming book on how evolution evolves. There's lots to keep you busy until the next newsletter after the holidays.

Enjoy!

MAs, PhDs, Fellowships

PhD in NCN-funded project "Philosophy of Science for the Replication Crisis"

The position offers a full 4-year scholarship, including funding for conference trips and equipment. The scholarship provides a net amount of 3466,9 PLN before the mid-term evaluation and 5340,9 PLN afterward, ensuring financial stability throughout the research period.

Project summary
The project focuses on the problem of conflicting results understood as an aspect of the replication crisis, where outcomes reported by methodologically sound and error-free studies remain in disagreement. ...

MAs, PhDs, Fellowships (cont.)

Uljana Feest suggested recently that failed conceptual replications are not necessarily a sign of the original result emerging from mistakes or errors what poses the question whether such replication failures undermine the original results. Feest's view on the replication crisis focuses on a narrower issue but the one that received limited attention from philosophers of science, i.e., on the problem of conflicting (recalcitrant) results. 'Conflicting results' denotes a situation where one study delivers evidence for a positive relationship between two phenomena (variables) or a positive treatment effect and another study suggests the two phenomena to be unrelated or even a negative sign of that relationship.

This problem can be understood as a sub-problem of the replication crisis, where two methodologically sound studies report effect sizes differing in size or even sign. The project approaches the problem of conflicting results and asks the following research questions: [RQ1] what is the concept of conflicting results? [RQ2] What are the epistemic factors boosting the emergence of conflicting results? [RQ3] What are the non-epistemic factors boosting the emergence of conflicting results? [RQ4] how data models (statistical models) represent? [RQ5] how to make inferences from conflicting results? [RQ6] what institutional contexts promote reproducible empirical research?

This research project involves using methods standard for philosophy (such as conceptual analysis and case study analysis), but also relies on a novel method of agent-based modeling, which has recently been successfully applied to address philosophy of science questions but has not been used to investigate the replication crisis so far. Conceptual analysis will be used to address the questions of what are conflicting results and what is the sense in which data models represent phenomena. Conceptual analysis and conceptual engineering will also be used to deepen the understanding of the sense in which data models represent. The main part of the project will rely on agent-based modeling to address epistemic and non-epistemic factors that influence the prevalence of conflicting results. Such models describe the behavior of represented agents (e.g., research teams) with simple rules and then simulate the behavior of and interactions among agents.

(more on next page...)

MAs, PhDs, Fellowships (cont.)

By comparing simulation results with different rules, the modeler learns which factors play a causally-relevant role in the simulated phenomenon. The advantage of agent-based modeling is that some characteristics of the simulated process might emerge that, due to its complexity, could not be studied with formal methods. Such models have been argued to be a tool useful for integrated history and philosophy of science. Agent-based modeling have been successfully used to study some problems in philosophy of science related to interactions among researchers.

Interested candidates are encouraged to contact the P.I. of the project, Dr. Mariusz Maziarz: mariusz.maziarz@uj.edu.pl

More info about the recruitment process will soon be published here:
https://filozofia.uj.edu.pl/en_GB/positions
https://filozofia.uj.edu.pl/pl_PL/ogloszenia/praca
https://human.phd.uj.edu.pl/en_GB/dla-kandydatow/rekrutacja-tryb-specjalny

Academic Jobs

LSE Philosophy - Hiring one or possibly more Fellows

The Department of Philosophy, Logic and Scientific Method is hiring an LSE Fellow in Philosophy. Salary from £40,229 to £48,456 pa inclusive of London allowance with potential to progress to £52,095 pa. This is a fixed term appointment for 24 months commencing 1 September 2024.

The Department of Philosophy, Logic and Scientific Method is committed to doing excellent research and teaching in philosophy in a manner that is continuous with the social and natural sciences and is socially relevant. It is also committed to creating an inclusive environment for philosophical debate that engages with a wide range of perspectives. It seeks to appoint an LSE Fellow who will, in a manner consistent with these commitments, contribute to the intellectual life of the Department and the School by contributing excellent, research-led undergraduate and master's-level teaching at the intersection of philosophy and the social sciences. ...

Academic Jobs (cont.)

The position will be for two years in the first instance, with the possibility of renewal for a third year. An ability to contribute to the teaching of at least one of the following courses is essential: PH240/PH440 Ethics of Data and AI and PH341 PPE Applications. An ability to contribute more broadly to the Department's teaching is desirable. The post permits substantial time for research, and the post-holder will be expected to contribute to the research culture and intellectual life of the department in their areas of specialization.

For those interested, please contact Alex Voorhoeve: a.e.voorhoeve@lse.ac.uk

Publications

Pradeu, T., Lemoine, L., Khelfaoui, M., and Gingras, Y. (2024). 'Philosophy in Science: Can Philosophers of Science Permeate through Science and Produce Scientific Knowledge?' *The British Journal for the Philosophy of Science*. https://doi.org/10.1086/715518

Sheehan, N., Botta, F. and Leonelli, S. (2024). 'Unrestricted Versus Regulated Open Data Governance: A Bibliometric Comparison of SARS-CoV-2 Nucleotide Sequence Databases'. *Data Science Journal*, 23: 29, pp. 1–29. https://doi.org/10.5334/dsj2024-029

Recent & Upcoming PiBM Events

PiBM Seminar Series

For those of you who missed it, or just want to revisit it, the video for Stefan Linquist's recent talk on "Genome-level Ecology" can now be found on the PiBM website: https://www.philinbiomed.org/event/stefan-linquist/

The next talks in this series will start up again in September or October. Stay tuned for some exciting speakers!

Recent & Upcoming PiBM Events (cont.)

Conference: The Microbiome and Biological Individuality, Bordeaux

This international and interdisciplinary conference will be held on **July 3rd, 2024** at the University of Bordeaux, France, in the historic city center of the vibrant city of Bordeaux (Pey Berland Campus).

It will gather a fantastic line-up of world-leading experts in microbiome research, for an in-depth discussion on the conceptual foundations of this field and its impact on how we conceive of biological individuality. For the full details, please visit the website: https://www.philinbiomed.org/event/microbiome-individuality/

Attendance is free to all, but registration is mandatory. If you would like to attend online, please contact Thomas Pradeu.

For those attending online, here is the Zoom link: https://u-bordeaux-fr.zoom.us/j/88367880201?pwd=3FydcJ63cQAaEtSEEPVJzHdQ56I8KA.1

This conference is organized by Thomas Pradeu, with the institutional support of the ImmunoConcEpT lab and the PhilInBioMed network, and the financial support of the Gordon and Betty Moore Foundation.

Online Discussions about Philosophy and Biology's Mutual Benefits

We are happy to announce an online documentary series about the philosophy of biology, and how biology and philosophy can work together, which includes extensive discussions with philosophers such as Paul Griffiths, Peter Godfrey-Smith, Alan Love, and many others.

To access the series, please visit: https://closertotruth.com/topic/philosophy-of-biology/

Reports on Recent PiBM Events

Reports from Participants in PiBM Summer School 2024

As was announced in earlier newsletters, the PiBM Summer School recently took place in Bordeaux. While the organizers felt quite strongly that it was a success, and greatly enjoyed doing it, here we have some reports from participants to give you and potentially interested future students an insider's perspective. The organizers greatly thank everyone for submitting their excellent reports!

Report By Doudja Boumaza, PhD Student, Institut de philosophie de Grenoble

As a PhD student in the philosophy of memory, I have always been passionate about science and find it difficult to combine science and philosophy in a research career. This is one of the reasons why I was intrigued when I saw the announcement of the "PhilinBioMed" summer school in my e-mail. My dissertation subject is based on the philosophy of biology, as I'm working on the function of memory, so I signed up for the course somewhat at random. Two months later, I was on the plane to Bordeaux, with relative peace of mind about my arrival, as the organisers had taken care of my travel tickets, accommodation and meals. From the very first day, I felt at home, finally understanding that it was possible - and even necessary - to use philosophy in science. The week was rich, intense, but one of the best for me since I started philosophy, I think. The week is organised around lectures that are both methodological and informative about the PinS method, but that also present the work of a researcher in the philosophy of science and science. A large part of the week is also devoted to group work in which we apply the PinS method to a given subject, under the guidance of fantastic researchers and teachers.

It was a truly enriching week, during which I met doctoral students, students and researchers with whom I was able to feed my thirst for knowledge (as well as a few glasses of wine... that's the speciality, after all!). To sum up, I'd go back with my eyes shut if I had the chance next year, and I hope that these exchanges will lead to future collaborations. As a memory worker, it was with fond memories that I returned to the fold.

Report By Coral González, PhD Student, Universidad de Granad

I couldn't be happier and more grateful for having been able to attend the PhilInBioMed Summer School 2024, which took place in Bordeaux earlier this month. First, I want to highlight the merit of the organizers, as they managed to bring together a diverse group of participants and speakers.

I particularly liked that the talks were divided into lectures by researchers, where they presented their work, and tutorial talks. The speakers at the summer school were truly fantastic. Renowned philosophers and academics, they brought a wealth of knowledge and experience to the sessions. Their enthusiasm and passion for philosophy were infectious, inspiring participants to delve deeper into their own philosophical inquiries. I appreciated that they always left enough time at the end of each talk for a Q&A session. As for the tutorials, they were really enlightening about what PinS are, how to apply them, and why philosophy is necessary in science. It seems to me that this is not an easy task, yet they managed to make it understandable for all kinds of audiences with different backgrounds, and they were really useful for the group projects we had to develop afterward.

In addition, the group work sessions were both fun and efficient. I am very pleased with my group, both with the group leaders and participants. There were participants with a more scientific background and others with a more philosophical background, but at no point did either side feel at a disadvantage. On the contrary, we managed to integrate both points of view, and the result was a very interesting project. Additionally, a very collaborative and supportive environment was created, where no one was superior to another, and thanks to that, I learned a lot and can say that I made good friends.

Another thing I really liked was that the course organized a gymkana throughout the city, which allowed us to get to know Bordeaux in greater depth and the other participants as well, as the scavenger hunt groups were different from the work groups. The wine and cheese night also helped us to get to know each other in a more relaxed setting. ...

I would also like to acknowledge the great dedication of the organizers and speakers, as they were with us throughout the entire course, during coffee breaks, meals, and work sessions. They were all very approachable and always available to talk to us about anything.

In conclusion, PhilInBioMed Summer School exceeded all my expectations. It is a unique experience that I would recommend to anyone passionate about the Philosophy of/in Science who has the opportunity. I leave there with my mind and heart full.

Report By Aurore Aymerie Dit Eymeric, PhD Student, Université Paris 1, Sorbonne

The PhilInBioMed Summer School was incredibly enriching, packed with inspiring intellectual encounters, engaging lectures, and thought-provoking debates. The lectures were highly specialized yet very accessible. Despite having no prior expertise in the fields covered, I was able to understand almost everything.

The lectures covered a wide range of topics, including immunology (Søren R Paludan, Thomas Pradeu), philosophy in phylogenetics (Matt Haber), neuroscience (Serge Ahmed), ecology (Marie Vasse), and neuropsychology (Carl Craver).

I especially enjoyed deepening my understanding of the PinS (Philosophy in Science) approach with the lectures on PinS (Jonathan Sholl), on the way to apply philosophical tools in PinS (Fridolin Gross) and on what PinS is not (Maël Lemoine).

Given that the angle of my thesis is very methodological since it has to do with building the appropriate tools and methodologies to answer questions of scientists about a marine research program, I must say that I found it very valuable to discuss the PinS approach, in particular the question of how to make contributions as a philosopher that are relevant to science and scientists. It gave me much food for thought. ...

The group work was another highlight for me. It offered us a great opportunity to exchange diverse perspectives, and collectively tackle complex problems, such as, in the case of my group, the emergence of biological individuality and the emergence of properties in multicellular organisms with guidance from our course leaders, Matt Haber and Marie Vasse.

Adjacent to the room used for lectures was another room where we took some coffee breaks, it was a very relaxing setting, with comfortable sofas and floor cushions. And let's not forget the gorgeous city we were in: Bordeaux is a warm and welcoming city with beautiful 18th century façades, an abundance of great restaurants and cafes. It was a delightful place to visit.

Thank you to the organisers of the PhilInBioMed Summer School for providing a welcoming environment in which participants from different backgrounds felt free to exchange their thoughts with each other as well as with the speakers and the organisers.

Detailed Report By Group 4 - AKA, The Biological Individuality Group

During the Bordeaux Summer School PhilInBioMed that took place from June the 3rd to June the 7th, participants were divided into groups that focused on different subjects according to their research interests and qualifications. The group I was in, Group 4, worked on the concept of biological individuality and the emergence of individuals in microbiology, more specifically in bacteria. It was composed of Yasmin Bar-Tzlil, Jonah Branding, Ge Fang and Cassandra Zie Yang, and I, Aurore Aymerie Dit Eymeric. We were supervised by Matt Haber and Marie Vasse.

Before coming to the summer school, we were given a few guiding questions by our supervisors. This was very helpful to start the discussion because none of us were experts on biological individuality or microbiology. Some of these questions included:

(to find out, see next page)

Reports on Recent PiBM Events (cont.)

- When should we regard groups of bacteria as individuals?
- More precisely, what sorts of behaviours do bacteria display that generate a collective identity as a new biological individual?
- What sort of criteria ought we employ to determine when groups of bacteria may be regarded as a biological individual?

With respect to these questions, we mainly focused on the issue of criteria and on whether or not biological individuality can come in degrees. Our initial lines of thought were threefold. The first one was to try to find temporal constraints or requirements for bacteria to become biological individuals. The second one was to draw inspiration from the philosophy of economics, in particular game theory, to try to characterize groups of bacteria into aggregates or true biological individuals by examining whether or not they had properties that could not be reduced to those of the individual bacteria within the group. The third one was to question the concept of biological individuality itself and to analyse whether it is a case of hyperdimensionality, where the different dimensions (e.g., boundaries, immunological individuality, evolutionary individuality) could overlap, or whether there are different concepts of biological individuality.

Our task during the summer school was to work together on a subject even without previous or little knowledge of the subject, to try to identify a scientific question within the literature, to propose philosophical tools that could help solve this question, and to suggest a scientific proposal detailing how we would try to solve the problem we identified.

In order to work on the emergence of individuals in microbiology, we decided to focus on the case of multispecies biofilms.

Multispecies biofilms are assemblages of microorganisms of different species that colonize a surface by attaching themselves to it by an extracellular polymeric substance matrix. The microorganisms become embedded within this self-produced extracellular matrix so that biofilms may serve as shelters for the bacteria within them. Indeed, the extracellular matrix serves as a protective layer against bacteriophages. ...

Biofilms facilitate physical adhesion (defined as bacteria sticking together) by producing extracellular polymeric substances (EPS) which creates a sort of sticky, gel-like matrix. This matrix is what enables the bacteria within the biofilm to stick together and to attach themselves to surfaces. The matrix also has the advantage of physically preventing access to host immune responses and to the action of antimicrobial agents. In view of this fact, biofilms provide immunological protection to the single bacteria of which they are composed. In addition, biofilms are heterogeneous structures wherein bacteria have the ability to create microenvironments in which different species or groups of bacteria occupy different niches and perform specific functions, such as breaking down complex organic compounds.

These observations have led us to question whether these traits are emergent properties of bacterial groups. If these characteristics are only seen in collective biofilms and not in individual bacteria, what implications does this have for defining a biological entity as an individual?

We suggested that studying the traits of single bacteria alongside the emergent properties of biofilms can provide a valuable model for examining the concept of biological individuality. By investigating biofilms, we aimed to determine whether emergent properties can be considered necessary or sufficient characteristics of biological individuals. We hoped this approach would enable us to apply insights gained from the biofilm model to other potential biological individuals.

This sums up the state of our reflection at the end of the fourth group session where we had to present a first draft. During the fifth group session, we exchanged with Thomas Pradeu who provided us with valuable insight.

Before presenting our scientific proposal, here is a detailed account of some of the most intriguing issues and questions we have identified regarding the emergence of properties within biofilms during the different group sessions.

(to find these issues, see next page!)

Reports on Recent PiBM Events (cont.)

A key issue we identified was that the emergent properties of a multicellular organism cannot be explained solely by the properties of single cells. By emergent property here, we mean features coming out of the interaction and organization of simpler units into a complex system—in this case, individual cells into a multicellular organism. Among the emergent properties of multicellular organisms that are important in this regard are tissue and organ formation, some specialized cell functions, and several complex behaviours, all of which result from interactions of coordinated cells and not from the action of any single cell. The evolution of similar emergent properties in multispecies biofilms could be useful in understanding the evolution of multicellularity.

Indeed, studying biofilms can help us get to know the mechanisms and evolutionary pressures behind the evolution of cooperative behaviours and complex organization in general. This could give insight into how multicellular organisms evolved, as well as some basic principles ruling emergent properties in biological systems.

Multispecies biofilms are aggregations of microorganisms of different species adhering to a surface and forming complex, structured environments. We think that they are good examples and models in the study of evolutionary altruism and symbiosis because they demand cooperation among individual bacteria to thrive. For example, maintenance of biofilm structure and function is dependent upon the investment of resources and energy by individual bacteria. This might be in the form of production of EPS, which literally hold the biofilm together, or perhaps the secretion of extracellular enzymes that will help degrade some nutrient for communal usage. They are, in this sense, forms of altruistic behaviour insofar as they benefit the biofilm community and not merely the bacteria that make the investment. Such a cooperative system can easily be exploited by 'cheating' bacteria. The cheaters would use the communal resources for the biofilm without contributing to their production, saving energy that would otherwise have been used for the common good. If not regulated, this extremely pervasive phenomenon in the biological world destabilizes systems of cooperation. Cheating behaviour, in most instances, and the mechanisms underlying enhanced cooperation despite the temptation to cheat are very important in a wide variety of practical applications.

...

Some insights into cooperative behaviour within the framework of conservation could be applied to the management of ecosystems and species interactions. Understanding how bacteria cooperate and 'cheat' in multispecies biofilms can help strategies seeking to treat chronic infections, as these biofilms are often resistant to antibiotic responses compared to free-living bacteria. Thus, biofilms not only provide a model to study basic biological principles but could also have important implications for different fields of research.

Analysing the mechanisms that promote cooperate in simple cellular coalitions has the potential to offer significant insights into 'defections' within higher eukaryotic systems— notably, cancer. We find that similar basic principles of cooperation and defection do prevail in most higher eukaryotic systems. For example, in a typical multicellular organism, a majority of cells cooperate among themselves for the common goal of ensuring the host's health and functionality. On the contrary, some cells deviate from this normal line of behaviour in cancer by defecting from such cooperation. Instead, they grow uncontrollably, thereby causing harm to the host organism despite being part of it. The information regarding these mechanisms might be difficult to obtain directly through studies on such complex systems; however, an understanding of similar processes can be achieved through an analysis of more simple systems like biofilms. Using biofilms as model organisms would provide researchers with a simpler yet more controllable context to study the basic principles of cellular cooperation and defection.

Greater insight into emergent properties of biofilms will follow from understanding how those features work and come into existence at many different spatial, temporal, and hierarchical scales. This is particularly important in establishing taxonomies for emergent characters, as it points out the similarities and differences between collective-level characteristics that are not reducible to the components they are composed of. Furthermore, just as in the case of bacterial biofilms, human societies, too, are composed of groups displaying emergent properties. Much like bacteria cooperate and compete within biofilms, human beings also engage in social structures and cultural systems that are not explainable by isolated individuals. ...

Thus, lessons learned from biofilm studies could provide an understanding of how and why social hierarchies or cultures have arisen and become maintained by individual members of human societies. This begs the question: can the insights gained from biofilms be applied to models of the origin and perpetuation of social hierarchies and cultural systems?

Moreover, biofilms can also act as helpful models for the realization of functional features so far identified solely in multicellular organisms, such as immunity and centralized information processing. Biofilms are communities of microorganisms that, in some cases, exhibit complicated behaviour and organization, and even rival functions found in higher-level, multicellular organisms.

One could consider the factor of immunity. In multicellular organisms, the immune system protects against infection and enables them to maintain internal stability. In a biofilm, collective defence behaviour can also be realised by the bacteria through the production of antimicrobial compounds to ward off external threats on the community. Such defence strategies in biofilms are interesting to study as it may reveal whether functions similar to the immune system exist at the level of the microbial community.

Centralized information processing would also be interesting to investigate. In multicellular organisms, the central nervous system processes information and coordinates the organism's responses. Although biofilms do not have a central nervous system, they can exhibit coordinated behaviours through communication methods like quorum sensing, where bacteria release and detect signalling molecules to regulate gene expression on a collective level. Investigating this could perhaps lead us to discover an equivalent of the central nervous system in biofilms.

This would have major implications in many fields. If we take the example of evolutionary biology, this could call into question the current understanding of the benefits of multicellularity and its evolution. Indeed, multicellularity is often thought to have evolved to achieve specific functions (e.g., enhanced defence mechanisms or complex information processing).

(you guessed it: next page!)

If these functions are found to be present in biofilms, it would suggest that these functions were not exclusive to multicellular organisms and may not have been the decisive factors driving the evolution of multicellularity.

Another point we raised was the importance of understanding the ecological and environmental contexts that influence the process of biofilm emergence. Whereas some biofilms could be considered an individual insofar as that they act as coherent unit, others could not be considered as such due to extremely high internal competitive levels. This variability in the degree of biofilm individuality is often related to the degree of competition among multispecies biofilms. In some cases, inter-species cooperation is so close that high individuality would be expressed, while in others, competition among species would be stronger and hence these communities would be less cohesive and more fragmented.

Based on Black et al.'s (2020) paper on ecological scaffolding—the way in which environmental structures support and shape biological processes— we wondered whether variations in the environment might explain part of the variation in biofilm individuality. This implies that we need to determine whether the level of cellular competition versus cooperation of single cells in a biofilm is influenced by the ecological context—for example, through resource availability, presence of stress factors, and habitat conditions. For instance, in situations characterized by nutrient-rich environments, with abundant resources, it's more likely that cooperation will be beneficial to the individual bacteria, and this could in turn lead to a strong manifestation of individuality in the biofilm. However, if resources are scarce, it's more likely that there will be less cooperation and that the biofilm would exhibit a looser type of structure.

Finally, we think investigating the mechanisms by which a biofilm develops spatial and temporal organization in the course of its development could yield interesting results. Biofilms are not simply aggregates, they are structured communities that change with time. We can use the philosophical framework of downward causation to investigate the role of structural constraints in evolution.

(their exciting proposal awaits!)

Reports on Recent PiBM Events (cont.)

Downward causation is the concept that a higher-level structures and their properties can influence and constrain the behaviour of lower-level constituents. In the case of biofilms, what it means is that the collective behaviour and organization of a biofilm can influence the activities of individual bacterial cells of which it is composed. One example of that would be quorum sensing, where bacterial cells in the biofilm communicate with one another by releasing and detecting certain signalling molecules called 'autoinducers.' When the concentration of autoinducers reaches a threshold, it triggers coordinated changes in gene expression and behaviour. Such coordination is an emergent property of the biofilm as a result of interactions among individual cells.

Niche construction in biofilms is another example of that. In this case, the bacteria, in a collective process, modify their environment to construct physical structures like protective shelters, that would be impossible for single cells to build. It shows how the biofilm as a whole affects the behaviour and performance of its single components. Looking at these and other examples can give us a better sense of the relative role of structural constraints and reciprocal causation in evolution.

This concludes the issues we discussed during the various group sessions.

Our main scientific proposal was that bottlenecks are a strategy to force cooperation within a group of cells and that they are necessary for something to be considered a biological individual, but that reproductive bottlenecks were not necessary, as they are too restrictive of a criterion and exclude groups of bacteria such as biofilms that should be considered biological individuals.

For something to be considered a biological individual, it has to be able to reproduce, through sexual reproduction or another way. To distinguish between reproduction and growth, we drew inspiration from Peter Godfrey-Smith's article, "The Evolution of the Individual" (2011), and found three parameters: the presence or absence of a bottleneck, the differentiation between germ and soma cells within a collective, and the overall integration within the collective. In Peter Godfrey-Smith's account, reproductive bottlenecks are an essential aspect of a biological individual. They are important because they are a means of dispersal, which is required to align the fitness of the individuals within a collective. ...

However, drawing on Black et al.'s paper, "Ecological scaffolding and the evolution of individuality" (2020), bacterial collectives do not go through reproductive bottlenecks but it's possible to consider that they go through ecological bottlenecks.

Since bottlenecks are an example of dispersal, we wondered whether dispersal could be another criterion for biological individuality. Indeed, dispersal is a strategy for cooperation, as is exemplified by biofilms. Insofar as biofilms are a common form of bacterial organisation found in nature, then we asked the question of whether bottlenecks should be replaced by dispersal in thinking about biological individuals.

As for philosophical tools, we thought about identifying and challenging core commitments within the existing literature with experimental results. We also considered revising Peter Godfrey-Smith's account of biological individuality and suggesting new experimental design.

The argument at the centre of our proposal was the following. In the literature, sexual reproduction by bottlenecks forms the basis of evolutionary individuality by contributing to cooperation between cells within the individual. However, the characteristics of biofilms are maintained and multiplied by dispersal rather than sexual reproduction. Biofilms can cooperate by dispersing structures that favour cooperation rather than by passing through reproductive bottlenecks. Therefore, we should consider that biofilms are biological individuals. If we do, then we would need to revisit Peter Godfrey-Smith's definition of what counts as a biological individual.

Thank you to all the organisers of the PhilInBioMed Summer School for providing us with the opportunity to work together on this subject, to Thomas Pradeu for his helpful comments during the process of exchange with a course leader from a different group, and to Matt Haber and Marie Vasse for their supervision.

PiBM Reflections

Philosophy in *Evolution Evolving (Part 1)*

By Kevin Lala, University of St Andrews

No field showcases the virtues of philosophy of biology more effectively than evolutionary science (although I recently learned from Gregory Rupik, 2024, that this observation is not necessarily a virtue). As a graduate student and would-be evolutionist in London in the late 1980s, I was introduced to the pioneering writings of David Hull on evolutionary epistemology, to Elliott Sober's brilliant 'The Nature of Selection' (1984), which stood ever since as a benchmark of great philosophy of science, to Susan Oyama's wonderfully rich and thought-provoking 'The Ontogeny of Information' (1985), and to Philip Kitcher's (1985) devastating 'Vaulting Ambition', which deconstructed human sociobiology. To a young researcher, like me, drawn to 'big questions' in science, these works were like nectar from the gods.

The stuff of my philosophy of biology upbringing may not qualify as philosophy 'in' biology, but it left me with a deeply entrenched admiration for what philosophers could contribute to my field, and that admiration has spawned many subsequent collaborations that brought philosophers directly into the scientific arena. Even that tribute short-changes the contributions that philosophers have made to my intellectual development, as over the decades an endless stream of savants have acted like a free consultancy service, ever willing to chew the intellectual cud. My career has entailed a journey, from reading and appreciating philosophy of biology, to consulting with philosophers, and finally to collaborating with them. In fact, my thoughts have been so enriched by philosophers that I could almost write a book on the subject. Perhaps one day I will, but just now I have a different book in mind.

Come September, Princeton University Press will publish a new book of mine, written together with Tobias Uller, Nathalie Feiner, Marcus Feldman and Scott Gilbert, entitled *Evolution Evolving: The Developmental Origins of Adaptation and Biodiversity*. You can think of it as an Extended Evolutionary Synthesis (EES) view of how adaptive evolution occurs, and the central role that developmental processes play in that. ...

PiBM Reflections (cont.)

Naturally, this means we address many conceptual issues – the origins of biological information, the utility of the genotype-phenotype distinction, the nature of biological causation, the sources of inheritance, and more – that I imagine would be of interest to readers of this newsletter. Given the strong philosophical thread running through our tome, I am very happy to get this opportunity to acknowledge the multiple contributions that philosophers of science have made to its inception. While here I share my story, my coauthors too have had extensive and productive interaction with philosophers, over many years: Scott Gilbert, for instance, has worked closely with Sahotra Sarkar, Marc Feldman with Lisa Lloyd, and Tobias Uller (with Kostas Kampourakis) recently edited a book on 'Philosophy of Science for Biologists' (2020). I have no doubt that these prior experiences of philosophy in biology have also enriched our writing.

The roots of *Evolution Evolving* I trace back at least to my time as a postdoc at UC Berkeley in the early 1990s, and the subsequent decade I spent in the Zoology department at Cambridge University. During that period, my co-conspirators John Odling-Smee, Marc Feldman and I were developing the theoretical foundations of niche construction theory, and John and I made regular visits to Stanford to work with Marc. I remember those typically month-long visits as being incredibly intense, with us laboring long hours, occasionally interspersed with visits to sit at the knee of other Stanford researchers, and pick their brains.

One such luminary with whom we had productive dialogue was Peter Godfrey-Smith, then on the Stanford philosophy faculty. Godfrey-Smith (1996) had distinguished between different types of explanation for the relationships between organisms and environments, which he had labelled 'externalist', 'internalist', 'constructive', and so forth. 'Externalist explanations' accounted for the internal properties of organisms in terms of environmental properties, while 'internalist explanations' described one set of internal properties of a system in terms of another set of internal properties, and 'constructive explanations' interpreted environmental properties in terms of the properties of organisms. ...

PiBM Reflections (cont.)

These distinctions helped us to conceptualise the key differences between how standard evolutionary theory explained the organism-environment relationship and how we wanted to describe that relationship in niche-construction terms. Standard theory provided externalist explanations, since the adaptations of organisms were explained relative to the properties of selective environments. In contrast, by stressing that the selective environments of organisms are part-dependent on the niche-constructing activities of organisms, we were proposing a mix of externalist and constructivist explanations, that Godfrey-Smith labelled 'interactionist'. Eventually we were to see niche construction theory as fitting into a bigger picture – a broader vision of the causal structure of evolution that is now often labelled the EES. With that came the recognition, now articulated in Evolution Evolving, that that the roots of adaptation are perhaps even more interactionist than we envisaged in our early works on niche construction, and that developmental processes always bias the phenotypic variation exposed to selection:

> "In continual interactive cycles, developmental processes bias what gets selected, but then selection modifies the developmental processes that create developmental bias. This process of reciprocal causation guides the evolution of morphology, and indeed all aspects of the phenotype. To disregard the causal role of development in evolution on the grounds that it is a product of selection, as is common, is questionable reasoning" (*Evolution Evolving*, p16).

Nowadays, we tend to speak of a commitment to 'reciprocal causation', but our thinking through the issues was greatly facilitated by those conversations with PGS. With the benefit of hindsight, I can see now that part of our conceptual struggle concerned the requirement to untangle a complex of interrelated questions, including: *How should biologists explain adaptation? What is an evolutionary cause?* And *Why do offspring resemble parents?* These issues took us years to resolve, but we were abetted by many philosophers of biology along the way. If PGS gets credit for helping us to get our heads around adaptation, then Kim Sterelny was likewise a catalyst for our views of evolutionary causation, and Paul Griffiths and Karola Stotz greatly aided our thinking on the nature of inheritance. ...

PiBM Reflections (cont.)

Lurking beneath these issues was a tentative and barely conscious commitment on our part to what is now labelled 'process ontology', which we picked up from Conrad Waddington's writings. In passing, we had flirted with concepts like 'homeorhesis' and 'autopoiesis', but – rightly or wrongly – had decided these labels had little explanatory utility to an audience of hard-nosed and often sceptical biologists that by-and-large were disappointedly uninterested in conceptual issues (at least, those conceptual issues we cared about).

In the early 2000s, we were invited to contribute to Susan Oyama, Russell Gray and Paul Griffiths' important volume, *Cycles of Contingency. Developmental Systems and Evolution* (2001), and also to give talks at a symposium on Richard Dawkins' extended phenotype concept organised by Kim Sterelny and Mateo Mameli at ISHPSSB in Vienna in 2003. Between them, these events allowed for extensive conversations with Kim Sterelny, but also Paul Griffiths, Susan Oyama, Evelyn Fox Keller, Mateo Mameli and Eva Jablonka. In those discussions the distinction between niche construction and the extended phenotype would always come up. The two ideas are superficially similar – after all, they are both concerned with how organisms construct artefacts and modify environmental states – but intellectually they are miles apart. Dawkins' treatment offers a traditional, gene-centric adaptationist account in which extended phenotypes are adaptations and the only selective feedback considered is to the genes that underly them. Conversely, niche construction theory offered a treatment that we can now regard as aligned with the EES: niche-constructed environments may (e.g. beaver dams) or may not (e.g. earthworm-processed soil) be adaptations, are often the product of extra-genetic inheritance (e.g. cultural niche construction), and can generate ecological feedback affecting selection at other loci, and in later generations (ecological inheritance). Philosophers of biology seemed to get very excited about this particular juxtaposition, and indeed in 2004 Sterelny invited me to debate Dawkins in the pages of *Biology & Philosophy* (Laland 2004; Dawkins 2004).

These exchanges with philosophers of biology – perhaps just over a decade of close interaction and dialogue – led to what was my first direct collaboration with a philosopher. ...

PiBM Reflections (cont.)

Sold, as I was, on the insight and clarity of thought that philosophers could bring to my arguments, I invited Kim Sterelny to coauthor an article that rebutted some commonly mooted criticisms of niche construction theory. The article, entitled "Seven reasons (not) to neglect niche construction", was published in the journal Evolution in 2006. Why I chose Kim, on reflection, was partly because, more-so than any other philosopher I knew, Kim was keen to be 'in' biology: that is, he wanted to be a participant in evolutionary debates, rather than just an observer and analyser. Over-and-above the intellectual assets that Kim brought to our partnership, the collaboration was a lot of fun. Kim, of course, is great company, and I had long had a weakness for staying up late drinking with him and discussing mighty topics. However, it was also fun because, as I said at the outset, I have always been searching for answers to fundamental questions, and my experience had been that philosophers, far more so than biologists, were often so inclined.

At that juncture in my career, I had really only been interacting with philosophers on the topic of niche construction, and within the bounds that perspective set. Not that those bounds were particularly restrictive: our work on niche construction had led us from population genetics, to ecosystem and community ecology, to various branches to the human sciences. I vividly remember a review of our book on niche construction from Paul Griffiths, that I can paraphrase as "8/10 for effort, but you really need to get into developmental biology". Having published a monograph that to me seemed almost suicidally broad, Paul's assessment seemed harsh. However, he was right of course, and further exchanges with Paul and Karola at conferences regarding developmental niche construction eventually led to John and I collaborating with Scott Gilbert to explore the parallels between niche construction and evo devo (Laland et al 2008). I think we were just beginning to suspect that the issues with which advocates of niche-construction theory were wrestling might be broader, and perhaps even more foundational, than we had thus far appreciated. Around 2011, those experiences primed me for a 'revelatory experience' that occurred while sitting with Gerd Müller under a tree at the KLI, and which was to shape the rest of my career. ...

PiBM Reflections (cont.)

It had become apparent to us that a major conceptual barrier to the acceptance of niche construction theory was Ernst Mayr's distinction between proximate and ultimate causation. In 1961, Mayr had published "Cause and effect in biology", a now classic article in Science that had influenced how most contemporary biologists understood causality. We had found that niche construction was frequently categorized as a proximate mechanism, and as a consequence was automatically disregarded as being evolutionarily significant. Worse, we were being told that we had muddled 'proximate' and 'ultimate' causation, when instead we were working with a different understanding of causation. Gerd and I both got very excited when I related this to him, and he explained that Mayr's distinction was no less a barrier to recognizing a role for developmental bias in evolution. Suddenly, we each realized that we had been fighting the same battle all these years!

Further discussion with John Odling-Smee and Tobias Uller led us to the view that several prominent current debates in biology – not just over evolution and development, and niche construction, but also over cooperation, and the evolution of language – were linked by a common axis of acceptance or rejection of Mayr's model of causation. As that year just happened to be the 50th anniversary of Mayr's paper, we saw an opportunity, and hurriedly pulled together a team of researchers to write up our thoughts as an article for Science. We argued that Mayr's formulation has acted to stabilize the dominant evolutionary paradigm against change but may now hamper progress in the biological sciences. Of course, for any such team to write with authority on causation we required a philosopher, so it seemed natural for us to invite Kim Sterelny on board.

That article brought us firmly into the terrain of wider debates about the explanatory utility of the dominant causal structure of evolutionary theory. Following our success in publishing "Cause and Effect in Science Revisited" (Laland et al 2011), Tobias Uller, John Odling-Smee and I got together a small interdisciplinary working group to think about and evaluate the concept of an extended evolutionary synthesis. The initiative was born partly out of frustration. ...

PiBM Reflections (cont.)

There had been a KLI workshop on the topic, organized by Massimo Pigliucci and Gerd Müller, at which John had participated, and the proceedings had been published as an edited volume (Pigliucci & Müller 2010). However, a lot of questions remained: *What was the EES?, Why was it needed?, How did it differ from the Modern Synthesis?, What findings motivated it?, What were its key assumptions and predictions?* We wanted answers to these questions, and since it seemed no one else was providing them, we set out to generate them ourselves, again assembling a team of experts in what we thought were the relevant fields. As our previous collaborations had been so successful, Sterelny was again our go-to philosopher – one brave (or foolhardy) enough to get 'into' biology and stick his neck out. After a couple of years of discussion, we eventually published our deliberations as a high-profile pair of articles: a short piece in Nature (Laland et al, 2014), and a more-protracted elaboration in *Proceedings of the Royal Society B* – the latter as the prestigious annual Darwin review (Laland et al 2015).

It is hard to overstate the impact of these papers: both have been cited well over 1000 times! While they were controversial at the time, I can't help but feel that that level of citation must mean something. Virtually all the ideas that the EES championed – plasticity-led evolution, extra-genetic inheritance, developmental bias, niche construction, evolvability – are now becoming, or have become, mainstream. Without those high-profile papers we probably would not have got a multi-million-pound grant from the John Templeton Foundation entitled "Putting the EES to the test". Tim Lewens and Massimo Pigliucci were key member of that EES research program grant, and many other philosophers were involved in more modest capacities, including Marta Halina, Jonathan Birch, Ellen Clarke, Kim Sterelny, Andrew Buskell, and Lynn Chiu. That grant, in turn, was phenomenally productive, leading to over 200 other scientific articles, many in top journals (see Chiu 2023 for a summary).

Yet for all those papers' success, it was apparent to us from an early stage that it would not be possible to make a truly compelling case for an extended evolutionary synthesis in article form. ...

PiBM Reflections (cont.)

This was a subject that required consideration of the history of biology, the philosophy of science, as well as an understanding of how development works, knowledge of evolutionary genetics, an appreciation of insights from various branches of theoretical biology, and comprehension of the avalanche of 'new biology' findings – particularly emanating from the burgeoning field of epigenetics. No, we would need a book length treatment. A decade later, *Evolution Evolving* is the result.

End Part 1 ... *(for more on Kevin's work, visit: **The Lala Lab**)*

You can find out more about *Evolution Evolving* (including content information, a Q&A with the authors, and some short animations illustrating key ideas) at the book website (https://www.evolutionevolving.org/). The website also provides a code offering readers who pre-order the book a 30% discount. Follow on social media (Twitter: @evoevolving LinkedIn: https://www.linkedin.com/in/profkevinlala/).

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PiBM Reflections (cont.)

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Looking ahead...

To everyone in the PiBM network, thanks again for all the great content shared throughout this academic year! This will be the last newsletter before the summer/ winter holidays but we will be back with more exciting PiBM news in August or September.

And, stay tuned for Part 2 of Kevin Lala's exciting essay in the next newsletter in which Kevin offers more snack-sized excerpts from the forthcoming co-authored book, *Evolution Evolving*. Enjoy your holidays!