

In Defense of the Organism.

Thomas Pradeu (Elizabeth Vitanza, trans.): *The Limits of the Self: Immunology and Biological Identity*. New York: Oxford University Press, 2012. ix+302 pp. ISBN: 978-0-19-977528-6, \$65 HB.

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Abstract

Thomas Pradeu's *The Limits of the Self* provides a precise account of biological identity developed from the central concepts of immunology. Yet the central concepts most relevant to this task (*self* and *nonsel*) are themselves deemed inadequate, suffering from ambiguity and imprecision. Pradeu seeks to remedy this by proposing a new guiding theory for immunology, the *continuity theory*. From this, an account of biological identity is provided in terms of uniqueness and individuality, ultimately leading to a defense of the heterogeneous organism as expressing the highest degree of individuality.

Organisms are under attack. Pathogens, environmental stress, and endogenous factors, among many others, threaten the survival of an organism. To persist, organisms must be able to mount an effective response, and a variety of strategies for regulating these stressors have evolved. Collectively, these are the immune system.

The organism is also under attack as a scientific concept. Samir Okasha (2011) has argued that *organism* is an anachronistic hierarchical rank, and that we should abandon this vestige of classification in favor of a rank-free ecological hierarchy. I have argued for a neighboring view (Haber 2013), observing that the term *organism*, much like *species*, is used to refer to a disparate group of entities, and that we ought to follow the lead of species eliminativists like Marc Ereshefsky (1992) and Brent Mishler (1999) and 'get rid of organisms'.

Thomas Pradeu's excellent *The Limits of the Self: Immunology and Biological Identity*

concerns both of these attacks. He proposes a new theory of immunology, *the continuity theory*, arguing it ought to replace existing theoretical frameworks in that field. From this, he develops a spirited defense of the organism as occupying a unique and theoretically relevant place in biology, providing a precise account of the organism as a heterogeneous entity expressing the highest degree of individuality.

Yet that does not quite do justice to Pradeu's book. Indeed, I think it embodies what philosophy of biology both has done well and should aspire to be. To draw this out, I will evaluate Pradeu's book along four dimensions, corresponding to what I view as four central projects in philosophy of biology: (1) identifying core commitments of biologists; (2) participating in conceptual debates *in* biology; (3) acting as science critics to *help* biologists; and (4) drawing on biology *for* philosophy.

The central task Pradeu sets himself is to provide a precise account of biological identity. His introductory chapter lays this out as two distinct problems, of *uniqueness* and *individuality*, warning against conflating the two. The former is presented as the question of what makes two entities different from one another, the latter a problem of delineation. Being distinctively unique means to have a character that no other entity has, e.g., a unique genome. Being a distinct individual, on the other hand, means having separate boundaries from other individuals, though other individuals may not be unique, e.g., monozygotic twins may be distinct individuals, despite not having unique genomes.

Immunology, Pradeu argues, can inform both of these problems of identity. There is vast diversity latent in immune systems, both at the immunogenetic level (in terms of genetic variation, recombination, and polymorphisms), and at the phenotypic level (e.g., in the proteins expressed by immune cells). Moreover, in organisms with adaptive immune systems, uniqueness will, in part, be constructed over time in relation to the antigens encountered by the organism. Thus the immune system is an active molecular record of the unique spatiotemporal location of different individuals. So, Pradeu concludes, "immune components are therefore one of the most convincing manifestations of each organism's uniqueness" (p. 7).

Pradeu, however, is primarily concerned with the immune system's role in individuation, both as it delineates the boundaries of organisms and in how it marks organisms as expressing the highest degree of biological individuality. Thus chapter 1, "Immunology, Self and Nonself," stakes out Pradeu's project. Immunology is characterized as including the study of biological identity, yet the central immunological concepts that appear most relevant for this task (*self* and *nonself*) are deemed inadequate, suffering from ambiguity and imprecision—Pradeu identifies five different meanings, though it is not always clear *which* of these immunologists are using. To be of use in our goal of specifying individuation conditions for organisms, Pradeu will need to refine, repair or replace these concepts. He opts for the latter, which

comprises the central task of the next four chapters.

In chapter 1 we get a definition of immunology, how that definition entails that all organisms have an immune system (supported by experimental cases drawn from vertebrate, invertebrate, plant, and microbial studies), and an initial account of the terms *self* and *nonself* as used in immunology. Pradeu defines immunology in terms of molecular reactions: immunology is “the discipline that studies specific interactions between immune receptors and antigenic patterns (ligands), interactions that can trigger mechanisms that destroy or prevent the destruction of target antigens” (p. 19). This is a departure from traditional definitions, which, loosely speaking, task immunology with studying the immune system as the variety of systems and strategies that evolved to respond to the stressors an organism might encounter (one member of our reading group preferred calling it “the ultimate kludge job”).

Pradeu’s molecular definition carries surprising consequences, simultaneously broadening and narrowing the scope of the field. Plants, invertebrates, and even microbes, on Pradeu’s definition, have immune systems. This nicely corresponds to recent molecular work in the field, and powerfully unifies a diverse set of phenomena across a broad phylogenetic scope. More boldly, the theory predicts these (and as yet undetected cases), rather than needing to account for them after the fact.

The taxonomy of objects under study by immunologists is not merely expanded, but revised. For example, the relevance of ‘specific’ versus ‘nonspecific’ immunity is greatly reduced: “There is immunity, properly speaking, only when there is a biochemically specific reaction between an antigen (ligand) and receptors carried by the immune system’s actors. Consequently, in my conception, the traditional distinction between ‘specific’ and ‘nonspecific’ immunity loses its relevance” (p. 20). Entities that were previously classified as distinct kinds of immunological actors fall under Pradeu’s unified definition. Specificity is simply a matter of scope, a measure of the ubiquity of an antigenic (molecular) pattern. Nonspecific actors simply react to specific patterns that are widespread in nature.

Other traditional components of the ‘nonspecific’ system get left out of the domain of immunology on Pradeu’s definition. Physical and mechanical boundaries such as epithelial tissue, respiratory mucous, or cell walls, on Pradeu’s definition, are not parts of the immune system because their interaction with antigens is not biochemically specific. Jettisoning these components from the domain of immunology is a tradeoff, though one that Pradeu moves over rather quickly. There is no substantive discussion of the costs of jettisoning these components from the field, though this may mark a radical departure for many immunologists.

The thin treatment of possible objections reflects what I think is the biggest weakness of the book, a sometimes limited consideration of counterarguments. For example, why not



replace immunology's specific/nonspecific classification with a molecular/non-molecular one? Pradeu provides the resources for offering principled reasons here (e.g., it would be too imprecise, or would undermine a unified application of the continuity theory), but relies on readers to make these connections. Some of this may be chalked up to Pradeu remaining focused on building a positive case for his view. So though the arguments would be strengthened at times by addressing concerns and counterarguments, avoiding these may simply reflect a methodological or strategic choice. The tight focus has its own benefits in providing clear and coherent arguments.

It is worth pausing to commend Pradeu on how clearly he lays out the field of immunology. The central concepts and arguments are complicated and driven by empirical details, requiring Pradeu to carefully spend time harnessing experimental results to make his case. This can be a challenge to the reader, yet he does this with extraordinary clarity, which goes a long way towards making those arguments accessible even to those less familiar with the field. This is all the more important for a field like immunology, which is driven as much by experimental details as by theory—a situation that Pradeu seeks to remedy. This also displays the value of carefully identifying the core commitments of a field, be they conceptual, experimental, ontological, methodological, or what have you. Pradeu's definition of immunology is not without controversy, but it is well-motivated and usefully advances the discussion.

The core commitments of biologists may also be characterized in terms of the research problems and projects they generate, and in how these subsequently shape a field. This is on clear display in chapters 2, "The Self-Nonsel Theory" and 3, "Critique of the Self-Nonsel Theory," which provide descriptions of the foundations of the self-nonsel theory and Pradeu's argument for why this theory is now inadequate, respectively. As in chapter 1, these are driven by a careful attention to experimental results and empirical data.

The self-nonsel theory is attributed to Frank Burnet. Although earlier immunologists employed the terms 'self' and 'nonsel', it is Burnet's usage that marks how these concepts are now employed. He treated the organism's differentiation of self fromonsel as a scientific problem in itself; as something to be explained, rather than as a self-evident starting point in immunology. This not only provided central guiding principles for immunologists, but also a central guiding research problem, i.e., it demanded that researchers answer the question of *how* an organism's immune system comes to recognize what is self andonsel. On this theory that distinction corresponds to the endogenous or exogenous origin of the antigen. This, in turn, provides a means of answering what Pradeu takes to be *the* central problem in immunology: determining the criterion of immunogenicity, of why and when an immune response is



triggered.

Burnet's self-nonsel theory of immunology generated a deeply fruitful and successful research program. Yet it also produced experimental data that Pradeu argues is inadequately explained by the self-nonsel theory. These have accumulated to the point of undermining the self-nonsel criterion of immunogenicity, with the most compelling being cases of autoreactivity (reaction to 'self') and immunotolerance (absence of response to 'nonsel'). The picture Pradeu paints is of a field left without a central guiding theory, instead relying on a collection of imprecise and vague concepts. Pradeu argues that this is bad for immunology, and that it will be more fruitful and productive with a new guiding theory.

Here we see Pradeu as the science critic. Much as a good film critic can help filmmakers make a better movie, philosophers of science help scientists practice better science.¹ This can take on a social aspect when philosophers identify (implicit or explicit) biases in scientific studies, noting how these may constrain, undermine, or distort the conclusions being drawn (see [Lloyd 2001](#) or [Richardson 2010](#) for exemplars par excellence). Or it can take the form of identifying what makes a particular case study a good or bad model of scientific reasoning, and what ought to be emulated (or not) of that study.

In *The Limits of the Self* this latter critical project is a subtle yet persistent and important theme of the book, defending the importance of a central guiding theory, or "organized set of testable explanatory and predictive statements," ([Pradeu et al 2013](#), p. 765, box 1, where this argument is placed more front and center). As the self-nonsel framework has been criticized in immunology, no general theoretical framing has emerged as a replacement. The problem, as Pradeu frames it, is that this leaves the field without unified guiding principles or research problems, and, more worryingly, without the resources to provide unified explanations of seemingly disparate data. Operating in the context of a guiding theory produces better science.

Perhaps valuing guiding theories this way sounds trivial, but it is not—especially for molecular and developmental fields of biology, where it is not obvious that there *are* always guiding theories (or that they are needed, or must be true to be useful, or would generate fruitful productivity; see [Fagan 2013](#)). This discussion takes place a bit in the background, and Pradeu's argument is one of demonstration. It is also compelling, and deserves to be taken seriously by critics of a theory-driven conception of science.

In chapter 4, "The Continuity Theory," Pradeu shifts from identifying the commitments of a field to actively participating in disputes over them, arguing that continuity theory should serve as immunology's guiding theory. First proposed by [Pradeu and Carosella](#)

¹Credit for this goes to David Magnus, who described the philosopher-as-science-critic this way in my first philosophy of science course. Thanks also to Bruce Glymour for reminding me of this very same point.



(2006a,b), the continuity theory holds that the criterion of immunogenicity—why and when an immune system is triggered—is the abrupt presence of novel antigens. Contrary to the self-nonsel self criterion of immunogenicity, whether these antigens are of exogenous or endogenous origin is irrelevant. This seemingly simple proposal carries substantial consequences. It offers a unified approach to a variety of features of immunological systems across a wide phylogenetic scope that are difficult to reconcile on the self-nonsel self theory, e.g., immunotolerance of exogenous antigens and autoreactivity. It generates a new set of research problems for immunologists to study, and a variety strategies for pursuing these that are obscured by a self-nonsel self framework.

The case Pradeu makes for the continuity theory is compelling, and the theory holds many attractions. For one, it demystifies the self-nonsel self distinction by articulating immunogenicity in clear molecular and mechanistic terms. It is also easy to reconcile with a view of the immune system as a regulatory system primarily concerned with maintaining homeostasis. This nicely coincides with an evolutionary treatment of these systems, yet firmly grounds immunology in developmental and molecular biology. And though the immune system is defined in terms of biochemical reactions, this is not a naïve reductionist account. To the contrary, Pradeu should be read as reviving what he identifies as an early commitment of the field that treats the organism more as an ecological whole rather than in terms of genomic expression (aligning himself with Burnet’s earlier work).

Not only is Pradeu’s case compelling, but there is evidence that the continuity theory is being taken up by immunologists: Elizabeth Jaffee appeals to it in order to explain what determines tumor immunogenicity (Blankenstein et al 2012); Hodge et al (2013) adopt the “criterion of continuity (CC)” as their definition of immunogenicity, “where immune cells respond to abrupt modifications of the antigenic patterns with which they are in contact” (p. 633, attributing this definition to Pradeu and Carosella 2006a); and Grignolio et al (2014) seek to incorporate it in their extension of the danger theory in their proposal of the ‘liquid self’ (though I would think this would be resisted by Pradeu). At the very least it appears that immunologists are taking the continuity theory very seriously, which means we philosophers ought to as well.

This advocacy continues into chapter 5, “Comparing the Continuity Theory to Other Immunological Theories,” where Pradeu considers his view against competing theories. The most prominent of these is Polly Matzinger’s danger theory (1994), which proposes, like the continuity theory, that it is not self-nonsel self recognition that generates an immune response, but danger (or, perhaps, damage). Pradeu identifies several problems with this theory, among them that ‘danger’ is both imprecise and ambiguous, and too anthropomorphic. Replacing it with ‘damage’ adds (some) precision, yet describes an immune *response*, not a *criterion* of immunogenicity, and so fails to provide



resources for explaining why and when an immune response is triggered. Pradeu also worries that danger theory retains the parts of self-nonsel theory that are inadequate (e.g., its “endogenous logic” p. 217), while rejecting those that should be retained (e.g., a criterion of immunogenicity).

Despite devoting just under half the chapter to danger theory, discussion of it feels a bit thin compared to the deep treatment offered of the self-nonsel theory. This is exacerbated by the absence of any discussion of DAMPs (Danger or Damage-Associated-Molecular-Patterns), which, at first pass, appear to provide an avenue for the danger theorist to defend their account against some of Pradeu’s complaints.² Let’s look at this in more detail.

Much as Pradeu defines the immune system in terms of molecular reactions between antigens and immune receptors, the danger theorist might do so in terms of biochemical reactions triggered by DAMPs. Danger, then, could be defined immunologically as the presence of these molecular patterns. Indeed, there are good empirical data supporting this in immune responses to both the endogenous (e.g., necroptosis of dying cells, [Kono and Rock 2008; Kaczmarek et al 2013]) and exogenous (e.g., fungal and bacterial pathogens in *Drosophila* [Chamy et al 2008]). Identification of DAMPs in various contexts, and when and whether reactions with these subsequently generate an immune response then become two of the central research problems for the danger theorist, providing a foundation for a rich research program.

This is not to say Pradeu does not have good arguments available to address this sort of response. Rather it is to observe that they are not on offer here, and that strikes me as a missed opportunity to expand the case for the continuity theory. For example, Pradeu might argue that a characterization of danger theory in terms of DAMPs is still empirically inadequate; or is narrower in scope than the continuity theory, which can offer a broader, unified account of phenomena that danger theory leaves unanswered; or that DAMPs are a feature of the immune system, rather than defining of them (some of these, and other more detailed responses, are in Pradeu and Cooper 2012).

Pradeu might have also argued that continuity theory subsumes danger theory. On a continuity account, there is nothing intrinsic about DAMPs that signal danger or damage, it is only by virtue of their abrupt novelty that an immune system response is triggered. Indeed, we should expect that organisms would have evolved some means of triggering the immune system, and the ability of cells to quickly produce novel antigens to signal homeostatic disruption or severe stress would be evolutionarily advantageous. There are experimental data supporting this, as at least some DAMPs appear to be functional intracellular proteins that, when released outside the cell upon tissue injury, become denatured, presenting as novel antigens (Rubartelli and Lotze 2007).

²Thanks to James Moore for this and other observations regarding DAMPs.



Furthermore, the continuity theory predicts that organisms should become acclimated to DAMPs if introduced gradually, repeatedly, and in small quantities (Pradeu 2012, p. 180, and elsewhere), whereas on the danger theory DAMPs should trigger a response regardless of mode of introduction. Framed this way, experiments to test between the theories can be imagined rather easily, e.g., early exposure to DAMPs may result in downstream failures of these to generate an immune response. This could also provide a means of explanation for any number of diseases, especially chronic late-onset conditions in which the immune system appears to fail to respond.

These five chapters culminate in the ambitious chapter 6, “What is An Organism? Immunity and the Individuality of the Organism,” which returns to the overarching topic: the problem of biological identity. Pradeu describes how his conception of immunology distinctively marks organisms as heterogeneous entities expressing the highest degree of individuality, how this subsequently challenges and enriches entrenched views in philosophy of biology, and stakes out important methodological challenges. Each is a substantial contribution worth reviewing. Let’s start with the last.

Pradeu is far from the first philosopher to tackle the problem of identity—about living things or otherwise. What’s distinctive is how he prioritizes experimental and theoretical support from the sciences to both frame and answer the critical questions at stake. His first move, after all, is to mine immunology for metaphysical insights. He identifies this approach as *scientific metaphysics*, (aligning himself with Ladyman and Ross 2007), seeing it as a straight-forward challenge to traditional philosophy: “Despite a long philosophical tradition that demands a total separation between ontology or metaphysics and experimental science, the link between the two seems to me close” (p. 220). In practice this means identifying the metaphysical commitments in our sciences, and to recognize that sometimes scientific theories are also philosophical ones. It might be tempting to simply call this naturalism, something like a demand that our metaphysical theories conform to our best science, and see it as relatively uncontroversial. After all, it seems that almost everyone today is a naturalist in this regard. Yet what Pradeu demands is a greater rigor than what many naturalists appear to aspire. Superficial engagement with the sciences is viewed as merely a cover, and insufficient for good metaphysics.

For philosophers of biology, scientific metaphysics should be familiar ground (even if we don’t always call it such). Pradeu rightly notes that there is a strong tradition in philosophy of biology of identifying the metaphysical consequences of evolutionary theory, and considering how metaphysics both impacts and is informed by experimental work. Pradeu seeks to extend this project to include physiology and molecular biology, by “showing to what extent immunology clarifies the metaphysical notions of identity, uniqueness, and individuality” (p. 221-2). This sets a high bar for

the level of precision, empirical detail, experimental sensitivity and sophisticated engagement with science that we should expect of our metaphysical theories.

Simultaneously, Pradeu is making a methodological plea to philosophers of biology to develop the field beyond a focus on evolutionary theory, reminiscent of O'Malley and Dupré's (2007) call for a more inclusive philosophy of biology that includes microbiology. Pradeu is extending that call, demonstrating how physiological and molecular fields—relatively underexamined by philosophers of biology—uniquely enrich, challenge, and add to our existing views.

Philosophers of biology, I think, are receptive this plea. The call for a more inclusive approach is a challenge that, in important ways, aligns well with the interests of those being challenged; whether and how fields of biology beyond evolutionary theory inform and conform to existing work in philosophy of biology reflects a natural growth of our field.³ My sense is that there is enthusiasm for work that branches out beyond the traditional focus, especially as scholars like Pradeu demonstrate how fruitful that may be. Graduate students seeking to make unique and meaningful contributions would do well to pay attention!

More resistance is likely in his call for scientific metaphysics. On the one hand, this is a challenge to contemporary metaphysics. It is not merely a charge of being too narrow, but of doing it wrong. It demands a highly sophisticated engagement with the sciences that few practice or have the training for. Yet it is also a challenge to philosophers of science resistant to doing metaphysics. It demands that those philosophers who *are* scientifically literate identify the metaphysical commitments in the sciences, and the perspectives that these bring to philosophy. In short, that we bridge the gap between the experimental sciences and metaphysics.

Yet Pradeu is not merely *telling* us how to draw on science for philosophy, he shows us as well. He treats the problem of identity as two distinct questions: that of *uniqueness* and *individuality*, and shows us how continuity theory enriches our conception of both. The immune system constructs a unique identity and delineates the boundaries of organisms. Replacing the self-nonsel criterion of immunogenicity with one of continuity means that both endogenous and exogenous entities will be parts of these living things, adding a heterogeneous dimension to how both uniqueness and individuality are expressed. Furthermore, the immune system is offered as part of the developmental system, “of the processes that build the living thing over time” (p. 225). This means that both uniqueness and individuality—and, thus, identity—will be expressed diachronically, come in degrees, and become more pronounced as a living thing persists. Moreover, Pradeu identifies work from immunology, microbiology, and

³Perhaps the focus on evolution is partly due to a founder effect. Imagine how our field might look had it grown out of immunology.



developmental biology that corresponds to this heterogeneous approach (p. 248), though this usage is even broader than he indicates. Human genomicists, for example, are adopting this heterogenous concept of organism and identity in just the way Pradeu describes, e.g., in describing how monozygous twins' genomes become more distinctive over time (Gringras and Chen 2001), and also in thinking about human microbiomes:

This [genetic and transcriptional] diversity [of the human gut microbiome], even between genetically identical individuals, provides an expanded view of our multicellularity and interpersonal genetic variation. (Turnbaugh et al 2010, 7508)

Other living things identities (e.g., species) will also be diachronic, come in degrees, and become more pronounced over time, though will lack an immune system, and, thus, a dimension of uniqueness and individuality. Pradeu argues that it is this distinct dimension of identity that permits the generation of the highest expression of individuality, citing three lines of argument: that the heterogeneous organism is a distinct entity with clearly defined boundaries, is an evolutionary individual, and controls lower-level variations (p. 255-62). What we are left with is a concept of the heterogeneous organism, distinctive among biological individuals, that expresses individuality to the highest degree.

Pradeu convincingly makes the case that the immune system permits the heterogeneous organism to express individuality in a distinctive way. Yet, other living things may also express distinctive dimensions of individuality, e.g., species may also be heterogeneous, though not due to the possession of immune systems (Haber 2012). This suggests that an argument analogous to Pradeu's may be available for other kinds of biological individuals. Namely, as with heterogeneous organisms, other living things may also express individuality along unique dimensions, and, on these measures, express it to a higher degree than the heterogeneous organism. So though Pradeu has made a compelling case that immunological individuals distinctively express individuality, and may do so to a high degree, *if* other dimensions of individuality are available, then which living things express individuality to the highest degree may depend on how we measure it. Of course, this is merely to suggest an argument, and to Pradeu's credit, the onus is on the critic to provide it.

The heterogeneous organism is presented as a direct challenge to the evolutionary criterion of individuality, which holds that "any entity upon which natural selection acts" is a biological individual (p. 234 and elsewhere). So (p. 255):

One of the implications of the evolutionary criterion of individuation is that the organism is only one level of biological individuality among others. ... [it] is not the only biological individual, nor a more important level of

individuality than any other.

How effective is this challenge? Notice, first, that Pradeu's target would more precisely be labeled a levels of selection account. This is certainly a popular account, and emphasizes how individuals at all levels function as units of selection. Indeed, [Wilson and Sober \(1989\)](#) exploit just this feature to defend multilevel selection (as do others, e.g., [Okasha 2006](#); [Godfrey-Smith 2009](#)). This emphasis, though, can come at the expense of recognizing what makes individuals at different levels distinct. Pradeu's goal is not to show that this stance is wrong or not useful, but to enrich it. The heterogeneous organism demonstrates the narrowness of the levels of selection framing, and how a richer evolutionary account is available by bringing physiological and developmental perspectives to bear on individuality.

I think Pradeu is right, both in his critique of the levels of selection approach being too narrow, and that a more inclusive account of individuality will be richer and more fruitful.⁴ And though the heterogeneous organism will certainly retain its distinctiveness, Pradeu's account of individuality will also generalize in what may be surprising ways—perhaps even in concordance with other more expansive treatments of biological individuality (e.g., from the systematics literature). These connections and consequences deserve to be explored in much more detail, but I suspect what we will find are, for example, *ranking* versus *grouping* debates about organisms analogous to those concerning higher taxa (e.g., [Mishler and Brandon 1987](#)), eliminativist accounts that hold the immunological organism up as the standard bearer for disambiguating the term 'organism', and a development of how degrees of individuality might be distinctively expressed across the biological scale.

Overall, the book is carefully written, well argued, deeply compelling, relevant and interesting. It is also difficult; Pradeu needs the details of immunology readily laid out in order to drive his argument, and this can be a challenge for those unfamiliar with recent developments in that field. Yet the reader will be rewarded for their work. The presentation is clear and accessible, without sacrificing precision.

When I invited people to join a reading group for this book, the biologist Fred Adler sent this reply: "This sounds like complete madness, and yet, somehow, fascinating."⁵ I took this to be (since confirmed) high praise of the project. It was also reminiscent of what Frédéric Bouchard once described to me as one of his favorite things about being a philosopher of biology, that we get to explore conceptual space that, for a myriad of reasons, biologists don't. Sometimes we discover things there that turn out to be of great value, and draw the attention of biologists in the process. Pradeu has done just this here. He takes on a highly ambitious project, and largely hits the mark. It is an

⁴Using a very different argument, I draw a very similar conclusion in my [2013](#).

⁵E-mail message to author, Feb. 5, 2013.

outstanding book, one I can wholeheartedly recommend.

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