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Forum

Looking beyond Popper: how philosophy can be relevant to ecology

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Current workflows in academic ecology rarely allow an engagement of ecologists with philosophers, or with contemporary philosophical work. We argue that this is a missed opportunity for enriching ecological reasoning and practice, because many questions in ecology overlap with philosophical questions and with current topics in contemporary philosophy of science. One obstacle to a closer connection and collaboration between the fields is the limited awareness of scientists, including ecologists, of current philosophical questions,

Synthesis

This paper emerges from a collaborative effort between ecologists and philosophers of science, initiated at a workshop aimed at improving research synthesis in ecology and related fields. Participants from the ecological community greatly valued the interaction with philosophers, discovering substantial commonalities and opportunities for collaboration. This contribution outlines the key outcomes of the workshop discussions. To foster future collaborations between ecologists and philosophers, we offer 1) practical examples the relevance of philosophical approaches to ecology, and 2) a directory of philosophers eager to collaborate with ecologists, complete with their contact details.

developments and ideas. In this article, we aim to overcome this obstacle and trigger more collaborations between ecologists and philosophers. First, we provide an overview of philosophical research relevant to ecologists. Second, we use examples to demonstrate that many ecological questions have a philosophical dimension and point to related philosophical work. We elaborate on one example – the debate around the appropriate level of complexity of ecological models – to show in more detail how philosophy can enrich ecology. Finally, we provide suggestions for how to initiate collaborative projects involving both ecologists and philosophers.

Keywords: bridging academic disciplines, ecological concepts, ecological modelling, epistemology, ethics, interdisciplinary work, methods in ecology, ontology

Introduction

For most contemporary ecologists, philosophy is rather disconnected from their research. Some ecologists probably wish they had more time to dive into philosophy; but this wish will most often stem from personal interest and be pursued outside working hours, if at all. In our experience, most ecologists are unaware of what philosophy of science has to offer to their worldview as scientists and to their research (Kampourakis and Uller 2020). While some ecologists know classic texts in philosophy of science, only few are aware of recent developments in the field. On top of that, philosophical texts are rarely written for (natural) scientists, covering topics beyond the measurable world and using language somewhat foreign to ecologists. While ecological concepts are increasingly addressed in the philosophical literature, the reverse is rarely the case.

One philosopher of science, Karl Popper, has been considered quite relevant for ecology (Strong 1980, Peters 1991) and features in several introductory textbooks (Pickett et al. 2007, Gibson 2015). Popper was interested in the methods of science, how scientific knowledge is developed, and how scientific work can be distinguished from pseudoscience. One of his most influential positions is the idea of falsification, according to which a scientific hypothesis should be testable in a strict sense, and should be rejected as soon as it is falsified, that is, as soon as empirical evidence reveals one instance incompatible with it (Popper 1968). A major inspiration for developing this suggestion was 20th century physics. It is important to note that Popper and his falsificationism are not universally embraced within philosophy (see Thornton 2023 for examples). Further, in a recent article, Raerinne (2024) argues that Popper has often been misinterpreted by ecologists, and that even if understood correctly, strict falsificationism is an unsuitable philosophy of science for ecology. He suggests that contemporary philosophy of science has more helpful approaches to offer to ecology.

Besides recurring, arguably rather sketchy references to Popper, ecology has always had strong implicit connections to philosophy. Scientific methods are deeply rooted in philosophical reasoning on how knowledge about the world can be produced – which is a major question in epistemology. Moreover, established rules for good scientific practice rest upon philosophical ideas about facts and norms, and thus involve ethical ideas. In addition, some highly influential ecological papers are rich with philosophical thinking. A good example of a publication that addresses ecological and philosophical questions simultaneously, and strongly influenced researchers in both disciplines, is Richard Levins' paper on 'The strategy of model building in population biology' (1966). This paper is cited in the population biology literature (Weisberg 2006a) and is discussed by philosophers even today (McCain and Kampourakis 2019, Beni 2022). In general, several ecological debates have had a philosophical element, from the debate on the utility of mathematical models in ecology (Mayr 1963, Haldane 1964, Simberloff 1981, Caswell 1988, Peters 1991) to the debate about the possible existence of ecological laws (Lawton 1999, Turchin 2001, O'Hara 2005, Dodds 2009). The recent evolution in the way data is analysed and inferences are drawn in ecology, from a more traditional hypothesis-testing approach to a model selection and multi-model inference methodology, has strong philosophical components as well (Burnham and Anderson 2002, Johnson and Omland 2004).

Links between ecology and philosophy therefore exist and reach beyond Popper's falsificationism. We believe, however, that these links could be much stronger. Philosophy of science has changed significantly since the work of Popper and an entire sub-field is dedicated to the philosophy of ecology. Such change is probably unknown to many ecologists. Accordingly, regular communication between ecologists and philosophers of ecology, leading to an ongoing exchange of ideas, is the exception rather than the rule. The current workflows in science usually do not allow ecologists to engage deeply with philosophical literature, collaborate intensively with philosophers, or attend philosophy conferences. A solution that seems timely and efficient is to build strong interdisciplinary teams of ecologists and philosophers to work on topics of mutual interest, thereby making collaboration a core component of research projects (see Kaiser and Müller 2021, Trappes et al. 2022, Kaiser et al. 2024 for results of such a collaboration). Such interdisciplinary collaborations can create reciprocal understanding and can motivate ecologists to 'think philosophically' beyond the collaborative project.

We recognize that initiating and maintaining interdisciplinary collaborations can be difficult or even unrealistic, especially when existing and potential connections between two fields are largely unknown. In what follows, we therefore highlight some key connections between the two fields with the aim of encouraging and helping to initiate future collaborations. First, we provide a brief overview of philosophical sub-fields that are particularly relevant to ecology, so that ecologists unfamiliar with current philosophy can get a better idea of what philosophy might offer. We then provide examples of ecological questions with a philosophical dimension, pointing to relevant philosophical literature. We elaborate on one case study to

demonstrate the potential for fruitful interactions between ecology and philosophy in greater detail. Finally, we provide suggestions for how to draw connections and promote collaboration between philosophy and ecology. All this is meant as an invitation for ecologists to 'try out' a little contemporary philosophy.

What philosophy can offer to ecology

Philosophers study a variety of topics, ranging from very broad and basic questions to quite specific and practical ones. With respect to ecology, three philosophical sub-fields are especially relevant: epistemology, ontology and ethics.

Epistemology: what do we know and how do we know it?

Epistemological questions are those related to knowledge, such as what counts as knowledge, how we acquire knowledge, what difficulties we face in the acquisition of knowledge, and how we can overcome them. Examples of epistemic questions commonly faced by ecologists include how to choose the best mathematical, statistical or conceptual model for a particular investigation; how many (and which) alternative hypotheses to consider in an experimental study; how to minimize effort while maximising statistical power; how to categorise data in the set versus outliers or noise; how to determine the transferability of results from one investigation to another; how to distinguish causal relations from mere correlations; how to interpret a failed prediction; and so on. More fundamentally, ecologists are increasingly wrestling with how to interact with different sources and forms of knowledge, including indigenous knowledge. Philosophers of science have dealt with many of these questions in an abstract way (Lipton 2005, Douglas 2009a, Cartwright 2012, Herfeld and Lisciandra 2019), but also in connection to actual scientific investigations, including ecological topics (McKay Illari et al. 2011, Justus 2021). These philosophical approaches can be regarded as resources with the potential to facilitate scientific practice in ecology, e.g. because they help understanding risks and difficulties that other scientists have faced in similar situations.

Ontology: what is there and how is it connected?

Ontology makes claims about which kinds of things exist in the world, what is their nature, and how they are related ('What is there?' Quine 1948). While epistemology aims to describe features of our knowledge or representations of reality, ontology concerns the general structure of reality (van Inwagen and Sullivan 2021). Ontology is a subfield of metaphysics, which includes additional questions, such as: what is necessary and what is possible? Only some ontological questions are relevant to ecology, but still, ecologists quite often face specific ontological questions. Examples include: 'what is an ecosystem/community/species/population/individual/ecological niche/mechanism?', calling for a specification of what these kinds of things are. Addressing these sorts of questions is often achieved by defining the related concepts and specifying their meaning. Philosophers of ecology have debated ontological and definitional issues concerning several basic ecological research units, such as community and ecosystem (Sterelny 2006, Eliot 2007, Odenbaugh 2007, Lean 2018a), biodiversity (Sarkar 2005), individual (Lidgard and Nyhart 2017, Kaiser and Trappes 2021), species (Hull 1978), or eco-evolutionary mechanisms (Kaiser and Trappes 2023). While many of these philosophical debates have probably gone unnoticed by ecologists, there are also examples of productive interdisciplinary collaborations on ontological topics (Krüger et al. 2021).

Ethics: what is right and what do (or should) we value?

Ethical issues are those related to what is right and wrong, how we should live our lives, and what we should value. Ethical and value-related questions relevant for ecologists include what sorts of scientific investigations are morally acceptable and ought to be pursued; to what extent and in what form one's values should influence scientific investigations; and how one should manage the natural environment given findings from ecology. Ecological research, especially in the context of practical applications, is inextricably linked to ethical debates. Examples include the values that form the very foundation of conservation biology (Soulé 1985, McShane 2017), how to consider the welfare of individual organisms versus species protection, for example whether individual organisms belonging to an invasive species should be killed in order to conserve native species (Rawles 2003, Turner 2023), whether species should be categorized into native and non-native species at all (Davis et al. 2011, Simberloff 2013), and debates around reintroductions and de-extinction (Sandler 2014, Browning 2018). These examples suggest that ecology and conservation biology can hardly be undertaken in a value-free manner. While a common view of scientific objectivity holds that values should not influence scientific research, many philosophers of science have presented arguments against this view (Kincaid et al. 2007, Douglas 2009b). For example, making a decision on accepting or rejecting a hypothesis on the basis of statistical significance means introducing a value decision on which significance level to choose, which itself depends on a judgment about how harmful different types of errors would be (Rudner 1953). Philosophers have developed scientifically informed accounts of 'when' and 'how' values can legitimately influence scientific research (Longino 1990, Odenbaugh 2021). However, philosophical work about values influencing science seems mostly disconnected from ecological science and practice (Jones 2021). This is a missed opportunity.

Fruitful integration of philosophy and ecology: examples

In the previous section, we introduced three major philosophical fields, suggesting areas in which they can be relevant to ecological research and the application of ecological knowledge. Now, we follow up by providing concrete examples of how philosophy can enrich ecological reasoning and practice (Table 1). Candidate topics are basic debates, for

Table 1. Examples for questions and challenges in ecology that have a philosophical dimension, with references to selected studies in the ecological and philosophical literature.

	Topic	Challenge in ecology	How philosophy could contribute	Ecological references	Connections to philosophy sub-fields	Philosophical references
1	Are there laws in ecology, and what are the limits to generalisations?	Ecologists often worry about the perceived lack of 'general laws' or 'laws of nature' in their discipline or sub-discipline	Philosophers have argued that laws in biology need not be universal and exceptionless but can be contingent and still useful as law-like generalisations. Ecological systems are complex and heterogeneous. Therefore, patterns sometimes break. In these cases, generalizations will also break. Moreover, it has been argued that laws are not necessary for successful science	Turchin 2001, O'Hara 2005, Linquist et al. 2016	Epistemology	Beatty 1995, Weber 1999, Woodward 2001, Mikkelson 2003, Mitchell 2003, Lange 2005, Elliott-Graves 2018, Pâslaru 2022, Elliott-Graves 2023
2	Should ecology strive for a grand unified theory?	In invasion biology, as an example, the absence of a unified theory has been regarded as a deficiency and an indicator for the field being not mature	Recent work in philosophy has shown that research fields can thrive even if they do not have a consistent, unified theory backing and guiding their research	Heger et al. 2021, Travassos-Britto et al. 2021	Epistemology	Love 2014, Elliott-Graves 2016
3	What constitutes a good explanation?	Explanations in ecology seldom follow a systematic scheme. Experienced ecologists have a clear idea of what is a good explanation. However, this is not made explicit, and can therefore be hard to grasp, e.g. for novices. Also, as long as these ideas are not made explicit, they cannot be discussed	Philosophers are interested in analysing what ecologists think a good explanation is (because they are interested in finding out how science works). Their analyses could in turn, help ecologists to openly communicate and discuss ideas on what is a good or useful explanation		Epistemology	Cooper 1993, Pâslaru 2009, Raerinne 2011, González del Solar et al. 2019
4	How to deal with uncertainty?	Uncertainty is ubiquitous in ecological research and environmental management and can have strong influences on the predictive ability and the acceptance of research results and management actions in society	Uncertainty can have different sources, leading to different kinds of constraints of scientific research. Distinguishing between different types of uncertainty can be helpful. In a cooperation between ecologists and philosophers, it has been suggested to distinguish between 'epistemic uncertainty' and 'linguistic uncertainty'. This can provide insights into the sources of uncertainty in ecology, and how to find adequate solutions. Additionally, there has been much discussion in environmental ethics and environmental management about how to make management decisions given uncertainty about evidence and future outcomes. The 'precautionary principle' has been influential but criticised by some philosophers	Regan et al. 2002, Latombe et al. 2019	Epistemology and ethics	Carnap 1945, Fine 1975, Putnam 1983, Shrader-Frechette and McCoy 1994

(Continued)

Table 1. Continued.

	Topic	Challenge in ecology	How philosophy could contribute	Ecological references	Connections to philosophy sub-fields	Philosophical references
5	Are neutral and niche models of ecological communities compatible?	The relative importance of neutral versus 'selective,' competitive or niche-based processes in community assembly has been controversial	Some ecologists and philosophers have argued in favour of accepting one model type, while others have argued for a pluralistic stance. In addition, philosophers have proposed a distinction between neutral or 'baseline' and null models, which has implications for model testing procedures	Strong 1980, Hubbell 2001, Vellend 2016	Epistemology	Beatty 1997, Bausman and Halina 2018, Bausman 2018, Morrow 2024a Sloep 1993, Wennekes et al. 2012, Zhang 2020, Odenbaugh (forthcoming)
6	(How) should evidence be weighted in meta-analyses?	In review studies and meta-analyses, empirical evidence is sometimes weighted to account for differences in study design (e.g. experimental versus observational, field versus laboratory), or studies following a certain design are excluded altogether. Such approaches assume that some methods are 'better' than others, and these value decisions become intermixed with the data themselves	Based on Levins 1966, Griesemer (2018) suggested that instead of weighting evidence and thus giving preference to either generality, realism or precision, evidential complexity could be mapped, displaying the distribution of empirical evidence along these three theoretical axes. Robustness analyses could help to assess the level of support for hypotheses	Example using evidence weighting: Heger and Jeschke 2014; response to Griesemer 2018: Heger and Jeschke 2018b	Epistemology	Levins 1966, Griesemer 2018
7	What are mechanisms in ecology?	In ecological research, mechanistic explanations are often regarded as a major aim; however, it remains unclear what is meant by 'mechanism', and which kinds of explanations are mechanistic. For instance, the term 'mechanism' is often used to refer to molecular or physiological processes in individuals. Whether there can also be individual-level ecological mechanisms is controversial	In philosophy of science, there is an ongoing debate about what mechanisms in biology are and what characterizes mechanistic explanations. Taking a closer look at these discussions can help refine the use of the term in ecology and improve mechanistic explanations	Heger 2022, Trappes et al. 2022	Ontology	Bunge 2004, Nicholson 2012, Pâslaru 2018, Potochnik 2020, Kaiser and Trappes 2023
8	What is a mechanistic model?	The term 'mechanistic models' is usually used without clear characterization of their differences to and advantages over other models. Consequently, the usefulness of mechanistic models has been underestimated in ecology	Definitions of the term 'mechanism' by philosophers (e.g. Craver, Glennan) helped ecologists to sharpen the term 'mechanistic model', thus allowing the discussion of advantages and risks of their application	Connolly et al. 2017	Ontology	Glennan 2017, Craver and Tabery 2019

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Table 1. Continued.

	Topic	Challenge in ecology	How philosophy could contribute	Ecological references	Connections to philosophy sub-fields	Philosophical references
9	How can organisms and individuals be defined and delimited?	There is a tendency in ecology to use the concepts of an individual and an organism without clearly defining them. Studies that apply inconsistent individuality criteria may have misleading results or be difficult to compare with other studies. For instance, field research on plants may have multiple incompatible methods available for individuating plants and/or estimating plant abundance	Philosophers have documented a great plurality of ways of individuating entities in biological research, such as individuals and organisms. Some philosophers argue for a single definition while others argue for pluralism. Either way, there is agreement on the importance of applying individuation criteria consistently within a study, and of considering potential implications of criterion choice	Harper 1977	Epistemology and ontology	Clarke 2010, Clarke 2012, Kovaka 2015, Pradeu 2016, Lidgard and Nyhart 2017, Kaiser and Trappes 2021
10	How can communities and ecosystems be defined and delimited?	Ecological collectives can be delimited in a variety of ways, and many think that delimitation methods are conventional. However, without applying clear and consistent delimitation methods, assessments and comparison of reference states, desired states and possible predictions of dynamics would be difficult or misleading	Ecologists and philosophers have proposed ways of delimiting ecological collectives. It has been suggested to distinguish between definition and description and to consider the respective purpose. Misleading management objectives and measures can thus be avoided	Jax et al. 1998, Jax 2007	Epistemology and ontology	Odenbaugh 2007 2010, Lean 2018b
11	What is a useful definition for 'ecological niche'?	Terms related to 'niche' (e.g. niche conservatism and niche breadth) have inconsistent meanings and usually lack clear definitions. Confusion of 'habitat' and 'environment' with 'niche' hinders usefulness of the niche concept for decision makers. What an individualized niche is and what are legitimate niche dimensions is often unclear	Work within ecology as well as in philosophy has focussed on clarifying the concepts related to 'niche' (and 'individualized niche') and on characterizing relationships or contrasts among definitions. Such work will increase awareness of the need for a conscious use of terms in relation to niche and will enhance communication in the future	Soberón 2007, Sexton et al. 2017, Sales et al. 2021, Trappes et al. 2022, Kaiser et al. 2024	Ontology	Griesemer 1992, Pocheville 2015, Trappes 2021, Morrow 2024b

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Table 1. Continued.

	Topic	Challenge in ecology	How philosophy could contribute	Ecological references	Connections to philosophy sub-fields	Philosophical references
12	Are the terms 'biodiversity', 'ecosystem services' and 'ecosystem functioning' value-laden?	The concepts 'biodiversity', 'ecosystem functioning' and 'ecosystem services' are widely used, but there is usually little awareness of their normative content. Different types of values are implicitly linked with these concepts, leading to controversies about definitions and conflicts in management (e.g., in conservation biology)	Respective work focusses on raising awareness of value dimensions, on the analytical distinction between (unavoidable) methodological values and (often implicit) moral values and suggests a clearer distinction of what is a matter of science and what of ethics	Nelson and Vucetich 2009, Jax 2010, Jax and Heink 2015, Horton et al. 2016	Epistemology and ethics	Longino 1990, Shrader-Frechette and McCoy 1993, Potthast 2000, Maier 2012, Maier and Feest 2016, Bocchi 2024
13	How should ecosystems be managed in a changing world?	Ecosystem managers have debated whether ecosystems should be managed primarily for functioning or for their composition; whether they ought to be restored to a prior state or managed in a forward-looking way, for instance to promote climate resilience; and how to balance ecosystem functioning against services needed by humans. In addition, the acceptability of 'novel ecosystems' is controversial.	Environmental philosophers have argued for and against several approaches to ecosystem management. One central issue (with relevance to novel ecosystems and other proposals such as managed relocation) is whether human influences should be accepted or reduced through management efforts. In addition, researchers have provided frameworks for incorporating differing values into environmental management decision-making.	DeFries et al. 2004, McCauley 2006, Schwartz et al. 2012, Arias-Arévalo et al. 2018, Higgs et al. 2018	Ethics	Callicott et al. 1999, Desjardins et al. 2019, Santana 2022, Millstein 2024
14	How should animal welfare and other ethical dilemmas be addressed in ecology and conservation?	Some ecological studies can involve harming or killing study organisms. Other studies involve transplanting organisms or otherwise manipulating communities in ways that could have unforeseen effects. In addition, eradicating 'invasive' or 'pest' populations is common practice in management work in order to reduce detrimental impacts of such populations.	Work on research ethics in biology has provided guidelines for ethical study design, such as weighing likely benefits of the research against likely harms, including harms to study organisms and ecosystems. A small amount of this work is devoted specifically to field research. In addition, environmental ethicists have debated whether and how to incorporate animal welfare concerns in environmental management	Farnsworth and Rosovsky 1993, Marsh and Kenchington 2004, Parris et al. 2010	Ethics	Callicott 1980, Crozier and Schulte-Hostedde 2015, Sandøe and Gamborg 2017

example about the role of laws and generalizations (example 1 in Table 1), the need for developing a unifying theory in ecology (example 2), or the challenge of uncertainty in ecological research and environmental management (example 4). Clarification of what basic ecological research units are (i.e. their ontology), definitions of ecological concepts and enhancement of their practical usefulness are further areas in which philosophical reasoning can enrich ecological research (examples 9–11). Philosophy can also help in re-considering common methodological approaches in ecology (example 5, 6) and can create ideas for improving scientific workflows or for enhancing conceptual precision (examples 7–8). Finally, philosophical input can be valuable when it comes to clarifying the extent to which common ecological concepts carry implicit evaluations (example 12), can offer guidance for decision-making (examples 4, 13) and can help to deal with ethical dilemmas, for instance in conservation (example 14). Most examples given in Table 1 point to ecological questions that have been debated in ecology as well as philosophy, as the references indicate. The question of what constitutes a good explanation (example 3), by contrast, is debated in philosophy of science, but we are not aware of parallel discussions in ecology (Pâslaru 2014).

For each of these cases, it would be interesting to further explore the current state of the debates, and to point out cases in which ecologists and philosophers have fruitfully interacted. Doing this is beyond the scope of this article though. We will instead elaborate on one example, which shows how philosophy is relevant for choosing the optimal level of complexity for ecological models.

Example: optimal model complexity

The debate on optimal model complexity clearly illustrates how deeply intertwined philosophy and ecology sometimes are (Sutherland et al. 2013, Travis et al. 2014, Ward et al. 2014, Chevalier and Knape 2020), and how philosophical perspectives can enrich discussions of ecological questions. In this debate, there is disagreement about how complex models ought to be in order to best conduct scientific investigations. While there is general agreement that ecological systems are complex (Levin 2005, Parrott 2010), there is less agreement about how to best approach this complexity in scientific investigations, especially in the context of modelling.

On one side are those who believe that a better understanding of complex systems can be gained by using simple models, i.e. those with few parameters (Wenger and Olden 2012, Marquet et al. 2014, Ward et al. 2014, Schindler and Hilborn 2015). The primary rationale is that reducing the inherent complexity of ecological systems makes them more tractable and thus easier to understand (Sugihara et al. 2012, Perretti et al. 2013, Chevalier and Knape 2020). A second motivation for reducing complexity is that this could allow scientists to distinguish between real causal factors, i.e. those that have a strong effect on ecological phenomena, and those with little or no effect, or noise (Strevens 2004). This, in turn, is meant to reduce the risk of overfitting models to data and therefore increase a model's predictive accuracy (Hitchcock and Sober 2004). Finally, one way of distinguishing between 'real causal factors' and 'noise' could be to identify which factors are common to many systems. In successful cases of generalisation, these common factors would be the 'real', generally applicable causal factors, so when the noisy, context-dependent factors are omitted, the remaining factors constitute the generalisation (Hitchcock and Sober 2004). Simple models, it has been argued, should therefore usually be rather general (Holling 1966, Strevens 2004).

On the other side are those who believe that the complexity of ecological phenomena should be reflected in models (Phillips et al. 2016, Essington et al. 2017, Fischer et al. 2018). The idea is that incorporating more data, parameters and detail yields more accurate representations of the system under investigation, which leads to more accurate explanations and predictions, which could in turn lead to more successful interventions. Advocates of this second view worry that what seem to be 'details' often turn out to be relevant causal factors, so omitting these from a model makes the model less predictively accurate (Travis et al. 2014).

The debate is not easy to resolve since both more and less useful models exist on either side, and it is not easy to arbitrate an overall ruling (Novak et al. 2011, Perretti et al. 2013, Ward et al. 2014). However, adopting a philosophical standpoint can help matters in two important ways. The first is by delving deeper into the theoretical foundations and assumptions of the views in the debate, to clarify them and re-examine their value. An example of this comes from Evans et al. (2013), a landmark paper in terms of collaboration between ecologists and philosophers, who provide a convincing argument against the (often implicitly accepted) equation 'simple = general = good' for ecological models, showing that complexity is a legitimate desideratum for some models, while demonstrating also that there are cases where adding complexity can make a model more general. These arguments seem to weaken the case for simple models by showing that if it is generality that we are after, then simple models are not necessarily the best option.

A second way to approach the debate is to question whether it needs to persist at all. This approach was adopted by Richard Levins (1966). Levins was notable in the sense that he was an ecologist who also seriously engaged with the philosophical literature, so he was able to adopt a philosophical approach to certain ecological problems (Levins 1993, Weisberg 2006b). The key insight of his 1966 paper is that modelers can have different aims when modelling, as they can desire their models to be general (i.e. apply to many different real-world systems), realistic (i.e. accurately represent the features of the phenomena under investigation, which corresponds to what people within the debate term 'high model complexity') or precise (i.e. to have finely specified outputs, usually in the form of predictions). In each model, scientists can maximise only two of the three desiderata, leading, in the extreme, to three modelling strategies and

three corresponding types of models (Odenbaugh 2003). Thus, Levins argued for pluralism, a position with a long history in philosophy of science (Mitchell 2003, Kellert et al. 2006). Another reason in favour of pluralism is that models can have a variety of functions in addition to generating predictions and explanations. For instance, models can be used to explore possibility spaces or to provide conceptual frameworks used within empirical work (Odenbaugh 2005). It is likely that different types of models are useful for these different aims.

Applied to ecology, a pluralist approach suggests that different research questions or different phenomena call for different models. Thus, there will be cases where generality is more important, others in which predictive accuracy is more important, and so on. Levins also suggested an alternative solution that bypasses the debate, namely to focus on models that are both general and realistic, but sacrifice precision. Using this strategy (and its models) is established in the ecological literature (Ramsey and Veltman 2005, Novak et al. 2011, Banitz et al. 2022), but still underrepresented (Justus 2005). A recent philosophical defence of this strategy and its usefulness for cases with limited or low-quality data can be found in Elliott-Graves (2020).

The pluralist strategy for modelling points to a topic that could benefit from future collaboration between ecologists and philosophers: the notion of robustness. Levins himself argued that in cases as the one described above, 'the truth is at the intersection of independent lies' (1966, p. 423), meaning that if models with independent assumptions converge in terms of their outputs, we can have greater confidence in these outputs. Subsequently, ecologists and philosophers have pointed out that this picture is rather simplistic (Weisberg 2006c, Parker 2011, Justus 2012). Philosophers have made conceptual progress by distinguishing between different kinds of robustness and identifying the advantages and disadvantages of each (Weisberg and Reisman 2008, Raerinne 2013) though many of these studies have focused on examples from other disciplines, e.g. climate science and economics (Kuorikoski et al. 2010, Parker 2011, Lehtinen 2018). We suggest that further collaboration between ecologists and philosophers on this topic might be useful for both disciplines.

This example illustrates that philosophical ideas and motivations are often present, albeit implicitly, in ecological research. Recognising them can help us understand why some debates exist or persist, and in some cases, can point to solutions. Our example shows two ways in which philosophical thinking can be integrated into ecological contexts. The first is where an ecologist, like Levins, who is well-versed in the relevant philosophical literature, explicitly adopts a philosophical approach to examine an ecological issue. The second occurs through collaboration between ecologists and philosophers, as in the case of Evans et al. (2013), where individuals bring their relevant expertise to the table with the aim of identifying and elucidating ecological issues. While we believe that, in principle, both approaches are of equal value, given the increase in volume and complexity of the literature in both philosophy and ecology since Levins's heyday, it will be practically more advantageous to opt for collaboration. For facilitating either way of making connections to philosophy, in the supplementary material we provide a list with reading recommendations, and a list of contemporary philosophers of ecology willing to be contacted by ecologists (Supporting information). Both lists are non-exhaustive and represent the interests and scientific networks of the team of authors, but we hope that they can serve as first points of contact to contemporary philosophers and respective literature.

Towards tighter connections

In the previous sections, we made suggestions for enhancing connections between ecology and philosophy, i.e. by creating interdisciplinary research projects on topics that are of ecological and philosophical interest or by individual efforts to become philosophically informed. Other suggestions are to participate in and contribute to conferences of the other discipline, hosting philosophers in biology labs, co-supervising PhD candidates, creating balanced curricula in both disciplines, holding joint journal clubs, and establishing new sections in journals to make room for philosophical and conceptual issues (Laplane et al. 2019). However, since academic life today is usually very busy, it could be argued that there is no room for engaging in any of these activities. With the previous sections, we wanted to invalidate this argument by providing examples that demonstrate how ecological tasks and topics often have implicit connections to and can profit from addressing philosophical questions. This means that in many cases, adding a philosophical perspective to ecological research is not as large a step as commonly believed. Collaborating with philosophers in these cases has the potential to strengthen the methodological and conceptual layer of ecological research by making the implicit philosophical reasoning more explicit.

A good way to facilitate personal interactions is the organization of workshops that bring together ecologists and philosophers of science, jointly focusing on a specific question, possibly including discussion formats that foster interdisciplinary exchange and perhaps a moderator trained in bridging different disciplines (e.g. with the help of design thinking techniques). Interdisciplinary work is always connected to challenges concerning different terminology, research cultures and methodologies. Workshops lasting several days spent together with much room for intensive discussion allow for time to get used to each other's disciplinary peculiarities and can help to promote the necessary mutual understanding. Discussions can then culminate in constructively commenting on each other's work (Griesemer 2018, Heger and Jeschke 2018a, b, Schurz 2021). The present article resulted from such an interdisciplinary workshop.

We hope that our contribution will serve as a catalyst, raising the interest of some ecologists in philosophy of science, and inspiring the development of collaborative research projects engaging both ecologists and philosophers. While the examples we have presented illustrate initial avenues for engagement, the

potential for interdisciplinary exploration is vast. We firmly believe that fostering personal connections and establishing joint research teams can be profoundly inspirational and rewarding. We envision a future where the integration of philosophy and ecology not only enriches ecological research but also advances the philosophical discourse. This synergy holds the promise of yielding innovative insights and solutions to pressing ecological challenges, emphasizing the imperative for greater integration and collaboration between these two fields.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Arias-Arévalo, P., Gómez-Baggethun, E., Martín-López, B. and Pérez-Rincón, M. 2018. Widening the evaluative space for ecosystem services: a taxonomy of plural values and valuation methods. – Environ. Values 27: 29–53.

Banitz, T., Schlüter, M., Lindkvist, E., Radosavljevic, S., Johansson, L. G., Ylikoski, P., Martínez-Peña, R. and Grimm, V. 2022. Model-derived causal explanations are inherently constrained by hidden assumptions and context: the example of Baltic cod dynamics position paper. – Environ. Modell. Softw. 156: 105489.

Bausman, W. and Halina, M. 2018. Not null enough: pseudo-null hypotheses in community ecology and comparative psychology. – Biol. Philos. 33: 30.

Bausman, W. C. 2018. Modeling: neutral, null, and baseline. – Philos. Sci. 85: 594–616.

Beatty, J. 1995. The evolutionary contingency thesis. – In: Wolters, G. and Lennox, G. (eds), Concepts, theories, and rationality in the biological sciences. Univ. of Pittsburgh Press, pp. 45–81.

Beatty, J. 1997. Why do biologists argue like they do? – Philos. Sci. 64: S432–S443.

Beni, M. D. 2022. Dosis sola facit venenum: reconceptualising biological realism. – Biol. Philos. 37: 54.

Bocchi, F. 2024. Metrics in biodiversity conservation and the value-free ideal. – Synthese 203: 45.

Browning, H. 2018. Won't somebody please think of the mammoths? De-extinction and animal welfare. – J. Agric. Environ. Ethics 31: 785–803.

Bunge, M. 2004. How does it work? The search for explanatory mechanisms. – Philos. Soc. Sci. 34: 182–210.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. – Springer.

Callicott, J. B. 1980. Animal liberation: a triangular affair. – Environ. Ethics 2: 311–338.

Callicott, J. B., Crowder, L. B. and Mumford, K. 1999. Current normative concepts in conservation. – Conserv. Biol. 13: 22–35.

Carnap, R. 1945. The two concepts of probability: the problem of probability. – Philos. Phenomenol. Res. 5: 513–532.

Cartwright, N. 2012. Presidential address: will this policy work for you? Predicting effectiveness better: how philosophy helps. – Philos. Sci. 79: 973–989.

Caswell, H. 1988. Theory and models in ecology: a different perspective. – Ecol. Modell. 43: 33–44.

Chevalier, M. and Knape, J. 2020. The cost of complexity in forecasts of population abundances is reduced but not eliminated by borrowing information across space using a hierarchical approach. – Oikos 129: 249–260.

Clarke, E. 2010. The problem of biological individuality. – Biol. Theor. 5: 312–325.

Clarke, E. 2012. Plant individuality: a solution to the demographer's dilemma. – Biol. Philos. 27: 321–361.
Connolly, S. R., Keith, S. A., Colwell, R. K. and Rahbek, C. 2017. Process, mechanism and modeling in macroecology. – Trends Ecol. Evol. 32: 835–844.
Cooper, G. 1993. The competition controversy in community ecology. – Biol. Philos. 8: 359–384.
Craver, C. F. and Tabery, J. 2019. Mechanisms in science. – In: Zalta, E. N. (ed.), The Stanford encyclopedia of philosophy metaphysics research lab. Stanford Univ.
Crozier, G. K. D. and Schulte-Hostedde, A. I. 2015. Towards improving the ethics of ecological research. – Sci. Eng. Ethics 21: 577–594.
Davis, M. A., Chew, M. K., Hobbs, R. J., Lugo, A. E., Ewel, J. J., Vermeij, G. J., Brown, J. H., Rosenzweig, M. L., Gardener, M. R., Carroll, S. P., Thompson, K., Pickett, S. T. A., Stromberg, J. C., Del Tredici, P., Suding, K. N., Ehrenfeld, J. G., Grime, J. P., Mascaro, J. and Briggs, J. C. 2011. Don't judge species on their origins. – Nature 474: 153–154.
DeFries, R. S., Foley, J. A. and Asner, G. P. 2004. Land-use choices: balancing human needs and ecosystem function. – Front. Ecol. Environ. 2: 249–257.
Desjardins, E., Donhauser, J. and Barker, G. 2019. Ecological historicity, novelty and functionality in the Anthropocene. – Environ. Values 28: 275–303.
Dodds, W. K. 2009. Laws, theories and patterns in ecology. – Michigan Publishing
Douglas, H. E. 2009a. Reintroducing prediction to explanation. – Philos. Sci. 76: 444–463.
Douglas, H. E. 2009b. Science, policy, and the value-free ideal. – Univ. of Pittsburgh Press.
Eliot, C. 2007. Method and metaphysics in Clements's and Gleason's ecological explanations. – Stud. Hist. Philos. Sci. C 38: 85–109.
Elliott-Graves, A. 2016. The problem of prediction in invasion biology. – Biol. Philos. 31: 373–393.
Elliott-Graves, A. 2018. Generality and causal interdependence in ecology. – Philos. Sci. 85: 1102–1114.
Elliott-Graves, A. 2020. The value of imprecise predictions. – Philos. Theor. Pract. Biol. 12: 004.
Elliott-Graves, A. 2023. Ecological complexity. – Cambridge Univ. Press.
Essington, T. E., Ciannelli, L., Heppell, S. S., Levin, P. S., McClanahan, T. R., Micheli, F., Plagányi, É. E. and van Putten, I. E. 2017. Empiricism and modeling for marine fisheries: advancing an interdisciplinary science. – Ecosystems 20: 237–244.
Evans, M. R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C. M., Merz, M., O'Malley, M. A., Orzack, S. H., Weisberg, M., Wilkinson, D. J., Wolkenhauer, O. and Benton, T. G. 2013. Do simple models lead to generality in ecology? – Trends Ecol. Evol. 28: 578–583.
Farnsworth, E. J. and Rosovsky, J. 1993. The ethics of ecological field experimentation. – Conserv. Biol. 7: 463–472.
Fine, K. 1975. Vagueness, truth and logic. – Synthese 30: 265–300.
Fischer, R., Rödig, E. and Huth, A. 2018. Consequences of a reduced number of plant functional types for the simulation of forest productivity. – Forests 9: 460.
Gibson, D. J. 2015. Methods in comparative plant population ecology, 2nd edn. – Oxford Univ. Press.
Glennan, S. 2017. The new mechanical philosophy. – Oxford Univ. Press.
Griesemer, J. 1992. Niche: historical perspectives. – In: Fox Keller, E. and Lloyd, E. A. (eds), Keywords in evolutionary biology. Harvard Univ. Press, pp. 231–240.
Griesemer, J. 2018. Mapping theoretical and evidential landscapes in ecological science: Levin's virtue trade-off and the hierarchy-of-hypotheses approach. – In: Jeschke, J. M. and Heger, T. (eds), Invasion biology. Hypotheses and evidence. CAB International, pp. 23–29.
Gonzáles del Solar, R., Marone, L. and Lopez de Casenave, J. 2019. Mechanismic approaches to explanation in ecology. – In: Matthews, M. R. (ed.), Mario Bunge: a centenary festschrift. Springer, pp. 555–573.
Haldane, J. B. 1964. A defense of beanbag genetics. – Perspect. Biol. Med. 7: 343–359.
Harper, J. L. 1977. Population biology of plants. – Academic Press.
Heger, T. 2022. What are ecological mechanisms? Suggestions for a fine-grained description of causal mechanisms in invasion ecology. – Biol. Philos. 37: 9.
Heger, T. and Jeschke, J. M. 2014. The enemy release hypothesis as a hierarchy of hypotheses. – Oikos 123: 741–750.
Heger, T. and Jeschke, J. M. 2018a. The hierarchy-of-hypotheses approach. – In: Jeschke, J. M. and Heger, T. (eds), Invasion biology. Hypotheses and evidence. CAB International, pp. 14–18.
Heger, T. and Jeschke, J. M. 2018b. The hierarchy-of-hypotheses approach updated – a toolbox for structuring and analysing theory, research and evidence. – In: Jeschke, J. M. and Heger, T. (eds), Invasion biology. Hypotheses and evidence. CAB International, pp. 38–48.
Heger, T., Jeschke, J. M. and Kollmann, J. 2021. Some reflections on current invasion biology, and perspectives for an exciting future. – NeoBiota 68: 79–100.
Herfeld, C. and Lisciandra, C. 2019. Knowledge transfer and its contexts. – Stud. Hist. Philos. Sci. 77: 1–10.
Higgs, E. S., Harris, J. A., Heger, T., Hobbs, R. J., Murphy, S. D. and Suding, K. N. 2018. Keep ecological restoration open and flexible. – Nat. Ecol. Evol. 2: 580.
Hitchcock, C. and Sober, E. 2004. Prediction versus accommodation and the risk of overfitting. – Br. J. Philos. Sci. 55: 1–34.
Holling, C. S. 1966. The strategy of building models of complex ecological systems. – In: Watt, K. E. F. (ed.), Systems analysis in ecology. Academic Press, pp. 195–214.
Horton, C. C., Peterson, T. R., Banerjee, P. and Peterson, M. J. 2016. Credibility and advocacy in conservation science. – Conserv. Biol. 30: 23–32.
Hubbell, S. P. 2001. A unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.
Hull, D. L. 1978. A matter of individuality. – Philos. Sci. 45: 335–360.
Jax, K. 2007. Can we define ecosystems? On the confusion between definition and description of ecological concepts. – Acta Biotheor. 55: 341–355.
Jax, K. 2010. Ecosystem functioning. – Cambridge Univ. Press.
Jax, K. and Heink, U. 2015. Searching for the place of biodiversity in the ecosystem services discourse. – Biol. Conserv. 191: 198–205.
Jax, K., Jones, C. G. and Pickett, S. T. A. 1998. The self-identity of ecological units. – Oikos 82: 253–264.
Johnson, J. B. and Omland, K. S. 2004. Model selection in ecology and evolution. – Trends Ecol. Evol. 19: 101–108.
Jones, E. 2021. Distinguishing regeneration from degradation in coral ecosystems: the role of value. – Synthese 199: 5225–5253.
Justus, J. 2005. Qualitative scientific modeling and loop analysis. – Philos. Sci. 72: 1272–1286.

Justus, J. 2012. The elusive basis of inferential robustness. – Philos. Sci. 79: 795–807.
Justus, J. 2021. The philosophy of ecology: an introduction. – Cambridge Univ. Press.
Kaiser, M. I. and Trappes, R. 2021. Broadening the problem agenda of biological individuality: individual differences, uniqueness, and temporality. – Biol. Philos. 36: 15.
Kaiser, M. I. and Müller, C. 2021. What is an animal personality? – Biol. Philos. 36: 1.
Kaiser, M. and Trappes, R. 2023. Individual-level mechanisms in ecology and evolution. – In: Bausman, W. et al. (eds), From biological practice to scientific metaphysics. Univ. of Minnesota Press, pp. 116–152.
Kaiser, M. I., Gadau, J., Kaiser, S., Müller, C. and Richter, S. H. 2024. Individualized social niches in animals: theoretical clarifications and processes of niche change. – BioScience 74: 146–158.
Kampourakis, K. and Uller, T. 2020. Philosophy of science for biologists. – Cambridge Univ. Press.
Kellert, S. H. et al. (eds) 2006. Scientific pluralism. – Univ. of Minnesota Press.
Kincaid, H. et al. (eds) 2007. Value-free science? Ideals and illusions. – Oxford Univ. Press.
Kovaka, K. 2015. Biological individuality and scientific practice. – Philos. Sci. 82: 1092–1103.
Krüger, O., et al. 2021. Individualised niches: an integrative conceptual framework across behaviour, ecology and evolution. – Eco.Evo.Rxiv. https://doi.org/10.32942/OSF.IO/7H5XQ.
Kuorikoski, J., Lehtinen, A. and Marchionni, C. 2010. Economic modelling as robustness analysis. – Br. J. Philos. Sci. 61: 541–567.
Lange, M. 2005. Ecological laws: what would they be and why would they matter? – Oikos 110: 394–403.
Laplane, L., Mantovani, P., Adolphs, R., Chang, H., Mantovani, A., McFall-Ngai, M., Rovelli, C., Sober, E. and Pradeu, T. 2019. Opinion: why science needs philosophy. – Proc. Natl Acad. Sci. USA 116: 3948–3952.
Latombe, G., Canavan, S., Hirsch, H., Hui, C., Kumschick, S., Nsikani, M. M., Potgieter, L. J., Robinson, T. B., Saul, W. C., Turner, S. C., Wilson, J. R. U., Yannelli, F. A. and Richardson, D. M. 2019. A four-component classification of uncertainties in biological invasions: implications for management. – Ecosphere 10: e02669.
Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.
Lean, C. H. 2018a. Indexically structured ecological communities. – Philos. Sci. 85: 501–522.
Lean, C. H. 2018b. Indexically structured eEcological communities. – Philos. Sci. 85: 501–522.
Lehtinen, A. 2018. Derivational robustness and indirect confirmation. – Erkenntnis 83: 539–576.
Levin, S. A. 2005. Self-organization and the emergence of complexity in ecological systems. – BioScience 55: 1075–1079.
Levins, R. 1966. The strategy of model building in population biology. – Am. Sci. 54: 421–431.
Levins, R. 1993. A response to Orzack and Sober: formal analysis and the fluidity of science. – Q. Rev. Biol. 68: 547–555.
Lidgard, S. and Nyhart, L. K. (eds). 2017. Biological individuality. Integrating scientific, philosophical and historical perspectives. – Univ. of Chicago Press.
Linquist, S., Gregory, T. R., Elliott, T. A., Saylor, B., Kremer, S. C. and Cottenie, K. 2016. Yes! There are resilient generalizations (or 'laws') in ecology. – Q. Rev. Biol. 91: 119–131.
Lipton, P. 2005. Testing hypotheses: prediction and prejudice. – Science 307: 219–221.
Longino, H. E. 1990. Science as social knowledge. Values and objectivity in scientific inquiry. – Princeton Univ. Press.
Love, A. C. 2014. The erotetic organization of developmental biology. – In: Minelli, A. and Pradeu, T. (eds), Towards a theory of development. Oxford Univ. Press, pp. 33–55.
Maier, D. S. 2012. What's so good about biodiversity? A call for better reasoning about nature's value. – Springer.
Maier, D. S. and Feest, A. 2016. The IPBES conceptual framework: an unhelpful start. – J. Agric. Environ. Ethics 29: 327–347.
Marquet, P. A., Allen, A. P., Brown, J. H., Dunne, J. A., Enquist, B. J., Gillooly, J. F., Gowaty, P. A., Green, J. L., Harte, J., Hubbell, S. P., O'Dwyer, J., Okie, J. G., Ostling, A., Ritchie, M., Storch, D. and West, G. B. 2014. On theory in ecology. – BioScience 64: 701–710.
Marsh, H. and Kenchington, R. 2004. The role of ethics in experimental marine biology and ecology. – J. Exp. Mar. Biol. Ecol. 300: 5–14.
Mayr, E. 1963. Animal species and evolution. – Belknap Press of Harvard Univ. Press.
McCain, K. and Kampourakis, K. 2019. What is scientific knowledge? An introduction to contemporary epistemology of science. – Routledge.
McCauley, D. J. 2006. Selling out on nature. – Nature 443: 27–28.
McKay Illari, P. et al. (eds) 2011. Causality in the sciences. – Oxford Univ. Press.
McShane, K. 2017. Is biodiversity intrinsically valuable? (And what might that mean?). – In: Garson, J., Plutynski, A. and Sarkar, S. (eds), The Routledge handbook of philosophy of biodiversity. Routledge, pp. 155–167.
Mikkelson, G. M. 2003. Ecological kinds and ecological laws. – Philos. Sci. 70: 1390–1400.
Millstein, R. L. 2024. The land is our community. Aldo Leopold's environmental ethic for the new millennium. – Chicago Univ. Press.
Mitchell, S. D. 2003. Biological complexity and integrative pluralism. – Cambridge Univ. Press.
Morrow, K. H. 2024a. Neutral and niche theory in community ecology: a framework for comparing model realism. – Biol. Philos. 39: 4.
Morrow, K. H. 2024b. Niches and niche models. – Br. J. Philos. Sci. doi: 10.1086/730329
Nelson, M. P. and Vucetich, J. A. 2009. On advocacy by environmental scientists: what, whether, why and how. – Conserv. Biol. 23: 1090–1101.
Nicholson, D. J. 2012. The concept of mechanism in biology. – Stud. Hist. Philos. Biol. Biomed. Sci. 43: 152–163.
Novak, M., Wootton, J. T., Doak, D. F., Emmerson, M., Estes, J. A. and Tinker, M. T. 2011. Predicting community responses to perturbations in the face of imperfect knowledge and network complexity. – Ecology 92: 836–846.
Odenbaugh, J. 2003. Complex systems, tradeoffs, and theoretical population biology: Richard Levin's "strategy of model building in population biology" revisited. – Philos. Sci. 70: 1496–1507.
Odenbaugh, J. 2005. Idealized, inaccurate but successful: a pragmatic approach to evaluating models in theoretical ecology. – Biol. Philos. 20: 231–255.
Odenbaugh, J. 2007. Seeing the forest and the trees: realism about communities and ecosystems. – Philos. Sci. 74: 628–641.
Odenbaugh, J. 2010. On the very idea of an ecosystem. – In: Hazlett, A. (ed.), New waves in metaphysics. Palgrave Macmillan UK, pp. 240–258.

Odenbaugh, J. 2021. Conservation biology. – In: Zalta, E. N. (ed.), The Stanford encyclopedia of philosophy, Spring 2021 edn. The Metaphysics Research Lab, Philosophy Department, Stanford University, Stanford, CA.
Odenbaugh, J. forthcoming. Neutrality, niche, and nulls: causal relevance in ecology. – In: Waters, C. K. and Woodward, J. (eds), Philosophical perspectives on causal reasoning in biology. Univ. of Minnesota Press.
O'Hara, R. B. 2005. The anarchist's guide to ecological theory. Or, we don't need no stinkin' laws. – Oikos 110: 390–393.
Parker, W. S. 2011. When climate models agree: the significance of robust model predictions. – Philos. Sci. 78: 579–600.
Parris, K. M., McCall, S. C., McCarthy, M. A., Minteer, B. A., Steele, K., Bekessy, S. and Medvecky, F. 2010. Assessing ethical tradeoffs in ecological field studies. – J. Appl. Ecol. 47: 227–234.
Parrott, L. 2010. Measuring ecological complexity. – Ecol. Indic. 10: 1069–1076.
Pâslaru, V. 2009. Ecological explanation between manipulation and mechanism description. – Philos. Sci. 76: 821–837.
Pâslaru, V. 2014. The mechanistic approach of the Theory of Island Biogeography and its current relevance. – Stud. Hist. Philos. Biol. Biomed. Sci. 45: 22–33.
Pâslaru, V. 2018. Mechanisms in ecology. – In: Glennan, S. and Illari, P. M. (eds), The Rutledge handbook of mechanisms and mechanical philosophy. Routledge, pp. 348–361.
Pâslaru, V. 2022. Laws of ecology and their promise of explanations. – Philos. Theor. Pract. Biol. 14: 5.
Perretti, C. T., Munch, S. B. and Sugihara, G. 2013. Model-free forecasting outperforms the correct mechanistic model for simulated and experimental data. – Proc. Natl Acad. Sci. USA 110: 5253–5257.
Peters, R. H. 1991. A critique for ecology. – Cambridge Univ. Press.
Phillips, R. P., Ibáñez, I., D'Orangeville, L., Hanson, P. J., Ryan, M. G. and McDowell, N. G. 2016. A belowground perspective on the drought sensitivity of forests: towards improved understanding and simulation. – For. Ecol. Manage. 380: 309–320.
Pickett, S. T. A. et al. 2007. Ecological understanding: the nature of theory and the theory of nature, 2nd edn. – Academic Press.
Pocheville, A. 2015. The ecological niche: history and recent controversies. – In: Heams, T., Huneman, P., Lecointre, G. and Silberstein, M. (eds), Handbook of evolutionary thinking in the sciences. Springer Netherlands, pp. 547–586.
Popper, K. R. 1968. Conjecture and refutation: the growth of scientific knowledge. – Harper & Row.
Potochnik, A. 2020. What constitutes an explanation in biology? – In: Kampourakis, K. and Uller, T. (eds), Philosophy of science for biologists. Cambridge Univ. Press, pp. 21–35.
Potthast, T. 2000. Bioethics and epistemic-moral hybrids: perspectives from the history of science. – Biomed Ethics 5: 20–23.
Pradeu, T. 2016. The many faces of biological individuality. – Biol. Philos. 31: 761–773.
Putnam, H. 1983. Vagueness and alternative logic. – In: Hempel, C. G., Putnam, H. and Essler, W. K. (eds), Methodology, epistemology, and philosophy of science: essays in Honour of Wolfgang Stegmüller on the occasion of his 60th birthday, June 3rd, 1983. Springer Netherlands, pp. 297–314.
Quine, W. V. 1948. On what there is. – Rev. Metaphysics 2: 21–38.
Raerinne, J. 2011. Causal and mechanistic explanations in ecology. – Acta Biotheor. 59: 251–271.
Raerinne, J. 2013. Robustness and sensitivity of biological models. – Philos. Stud. 166: 285–303.
Raerinne, J. 2024. Popperian ecology is a delusion. – Ecol. Evol. 14: e11106.
Ramsey, D. and Veltman, C. 2005. Predicting the effects of perturbations on ecological communities: what can qualitative models offer? – J. Anim. Ecol. 74: 905–916.
Rawles, K. 2003. Conservation and animal welfare. – Global Bioeth. 16: 99–109.
Regan, H. M., Colyvan, M. and Burgman, M. A. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. – Ecol. Appl. 12: 618–628.
Rudner, R. 1953. The scientist qua scientist makes value judgments. – Philos. Sci. 20: 1–6.
Sales, L. P., Hayward, M. W. and Loyola, R. 2021. What do you mean by "niche"? Modern ecological theories are not coherent on rhetoric about the niche concept. – Acta Oecol. 110: 103701.
Sandler, R. 2014. The ethics of reviving long extinct species. – Conserv. Biol. 28: 354–360.
Sandøe, P. and Gamborg, C. 2017. Animal welfare impact assessments: a good way of giving the affected animals a voice when trying to tackle wild animal controversies? – J. Agric. Environ. Ethics 30: 571–578.
Santana, C. G. 2022. The value of and in novel ecosystem(s). – Biol. Philos. 37: 6.
Sarkar, S. 2005. Biodiversity and environmental philosophy: an introduction. – Cambridge Univ. Press.
Schindler, D. E. and Hilborn, R. 2015. Prediction, precaution and policy under global change. – Science 347: 953–954.
Schurz, G. 2021. The hierarchy-of-hypotheses approach in a philosophy of science perspective. – BioScience 71: 350–356.
Schwartz, M. W. et al. 2012. Managed relocation: integrating the scientific, regulatory and ethical challenges. – BioScience 62: 732–743.
Sexton, J. P., Montiel, J., Shay, J. E., Stephens, M. R. and Slatyer, R. A. 2017. Evolution of ecological niche breadth. – Annu. Rev. Ecol. Evol. Syst. 48: 183–206.
Shrader-Frechette, K. and McCoy, E. D. 1993. Method in ecology. Strategies for conservation. – Cambridge Univ. Press.
Shrader-Frechette, K. S. and McCoy, E. D. 1994. Biodiversity, biological uncertainty, and setting conservation priorities. – Biol. Philos. 9: 167–195.
Simberloff, D. 1981. The sick science of ecology: symptoms, diagnosis and prescription. – Eidema 1: 49–54.
Simberloff, D. 2013. Introduced species, homogenizing biotas and cultures. – In: Rozzi, R. et al. (eds), Linking ecology and ethics for a changing world: values, philosophy, and action. Springer Netherlands, pp. 33–48.
Sloep, P. B. 1993. Methodology revitalized? – Br. J. Philos. Sci. 44: 231–249.
Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – Ecol. Lett. 10: 1115–1123.
Soulé, M. E. 1985. What is conservation biology? – BioScience 35: 727–734.
Sterelny, K. 2006. Local ecological communities. – Philos. Sci. 73: 215–231.
Strevens, M. 2004. The causal and unification approaches to explanation unified: causally. – Noûs 38: 154–176.
Strong, D. R. 1980. Null hypotheses in ecology. – Synthese 43: 271–285.
Sugihara, G., May, R., Ye, H., Hsieh, C. H., Deyle, E., Fogarty, M. and Munch, S. 2012. Detecting causality in complex ecosystems. – Science 338: 496–500.

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C. and Hails, R. S. 2013. Identification of 100 fundamental ecological questions. – J. Ecol. 101: 58–67.

Thornton, S. 2023. Karl Popper. – In: Zalta, E. N. and Nodelman, U. (eds), The Stanford encyclopedia of philosophy, winter 2023 edn. The Metaphysics Research Lab, Philosophy Department, Stanford University, Stanford, CA.

Trappes, R. 2021. Defining the niche for niche construction: evolutionary and ecological niches. – Biol. Philos. 36: 31.

Trappes, R., Nematipour, B., Kaiser, M. I., Krohs, U., van Benthem, K. J., Ernst, U. R., Gadau, J., Korsten, P., Kurtz, J., Schielzeth, H., Schmoll, T. and Takola, E. 2022. How individualized niches arise: defining mechanisms of niche construction, niche choice, and niche conformance. – BioScience 72: 538–548.

Travassos-Britto, B., Pardini, R., El-Hani, C. N. and Prado, P. I. 2021. Towards a pragmatic view of theories in ecology. – Oikos 130: 821–830.

Travis, J., Coleman, F. C., Auster, P. J., Cury, P. M., Estes, J. A., Orensanz, J., Peterson, C. H., Power, M. E., Steneck, R. S. and Wootton, J. T. 2014. Integrating the invisible fabric of nature into fisheries management. – Proc. Natl Acad. Sci. USA 111: 581–584.

Turchin, P. 2001. Does population ecology have general laws? – Oikos 94: 17–26.

Turner, C. 2023. On the fundamental incompatibility between wildlife conservation and animal ethics. – S. Afr. J. Philos. 42: 261–269.

van Inwagen, P. and Sullivan, M. 2021. Metaphysics. – In: Zalta, E. N. (ed.), The Stanford encyclopedia of philosophy metaphysics research lab. Stanford Univ.

Vellend, M. 2016. The theory of ecological communities. – Princeton Univ. Press.

Ward, E. J., Holmes, E. E., Thorson, J. T. and Collen, B. 2014. Complexity is costly: a meta-analysis of parametric and non-parametric methods for short-term population forecasting. – Oikos 123: 652–661.

Weber, M. 1999. The aim and structure of ecological theory. – Philos. Sci. 66: 71–93.

Weisberg, M. 2006a. Forty years of 'the strategy': Levins on model building and idealization. – Biol. Philos. 21: 623–645.

Weisberg, M. 2006b. Richard Levins' philosophy of science. – Biol. Philos. 21: 603–605.

Weisberg, M. 2006c. Robustness analysis. – Philos. Sci. 73: 730–742.

Weisberg, M. and Reisman, K. 2008. The robust Volterra principle. – Philos. Sci. 75: 106–131.

Wenger, S. J. and Olden, J. D. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. – Methods Ecol. Evol. 3: 260–267.

Wennekes, P. L., Rosindell, J. and Etienne, R. S. 2012. The neutral – niche debate: a philosophical perspective. – Acta Biotheor. 60: 257–271.

Woodward, J. 2001. Law and explanation in biology: invariance is the kind of stability that matters. – Philos. Sci. 68: 1–20.

Zhang, M. 2020. The use and limitations of null-model-based hypothesis testing. – Biol. Philos. 35: 31.