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1 Introduction

Why should we care about ecological complexity? This question can be understood in two ways, depending on whether the emphasis is placed on the word ‘ecological’ or the word ‘complexity’. We could be asking why we should care about complexity as it manifests in ecology, rather than how it manifests in other disciplines. Alternatively, we could be asking why, of all the issues in ecology, we should focus on complexity. It turns out that these two questions are closely connected; what makes *complexity* in ecology interesting is also what makes complexity in *ecology* interesting. The short answer is *causal heterogeneity*: the variability of causal factors over space or time. In what follows, I will argue that causal heterogeneity is an important but hitherto undervalued dimension of complexity. It is important because it explains some of the most pressing difficulties faced by practicing ecologists, namely generalisation, prediction and intervention in ecological systems. A re-conceptualisation of complexity that includes causal heterogeneity can give us a better understanding of these problems.

The idea that complexity creates difficulties for scientific practice is neither new nor limited to ecology. It features prominently in the debate about laws in biology, as it explains why most generalisations in biology fall short of the standards of ‘lawhood’ (Mitchell 2003). Biological systems are complex in the sense that they contain numerous causes whose interactions lead to configurations that are contingent on historical factors. As a result, any generalisations that describe them are neither universal nor exceptionless (Mitchell 2003). This has been a conspicuous thorn in the side of many biologists and philosophers of biology, as historically, laws were considered to be the hallmarks of true science. Any discipline that did not have laws of nature was at best immature and at worst not truly scientific.

While some biologists and philosophers gave up on the idea of biological laws completely (e.g. Lawton 1999, Shrader-Frechette & McCoy 1993)[1], others argued that if laws in biology do not conform to our pre-existing conception of lawhood, then the fault lies with this conception; the answer is to revise our notion of lawhood so that it captures biological laws (Mitchell 2003, Woodward 2001). In the words of Sandra Mitchell, the plurality of causes in evolutionary biology is ‘not an embarrassment of an immature science, but the mark of a science of complexity’ (2003, p. 115). Here, Mitchell succinctly highlights the two main issues of biological complexity: that complexity is a key way in which

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[1] Not everyone interpreted the absence of laws in biology as equally problematic. For instance, Shrader-Frechette and McCoy (1993) argued that the absence of laws did diminish the scientific status of biology.

biology differs from other sciences and that this does not mean that biology is deficient or inadequate when compared to these other sciences.

Ecological systems are biological systems and thus share most of the features of biological complexity along with the difficulties it generates. However, ecological systems are special in the sense they are also characterised by pervasive *causal heterogeneity*. Causal heterogeneity exacerbates and compounds the difficulties generated by biological complexity: not only do ecological systems contain numerous causes, but these causes are also diverse and variable. This means that even the generalisations that are present in evolutionary biology might be elusive in ecology. Thus, a thorough investigation of *ecological complexity*, with causal heterogeneity as one of its key features, is important for gaining a deeper understanding of some of the most important problems faced by practicing ecologists. In addition, it can help us gain a more comprehensive understanding of scientific practice, as understanding ecological complexity can serve as a blueprint for a better understanding of complexity in other disciplines where causal heterogeneity also features prominently.

But how important is ecological complexity *really*? Is rarity or absence of laws merely a philosophical problem or does it also affect the practice of ecology? The effects of complexity are far reaching for ecological practice *and* for the theoretical foundations of the discipline. I will illustrate the practical effects of complexity in the next section, by showing that complexity can lead to *surprises* in ecological research. I will then show that frequent surprises have dangerous theoretical implications, as they are used by some scientists and philosophers to cast doubt on the overall quality of ecological research and the scientific status of the discipline itself.

1.1 Surprise!

While investigating the effects of bird guano runoff on intertidal ecosystems in southwestern South Africa, a group of scientists observed that two neighbouring islands (4 kilometres apart) had very different benthic communities: one was teeming with lobsters while the other was covered in mussels and whelks. According to the local fishermen, lobsters were present in both locations till the early 1970s, but then mysteriously disappeared from the second island. After a series of horror-inducing experiments, where lobsters were re-introduced to the second island, the scientists realised that the whelks had turned the tables on their erstwhile predators and now preyed on the lobsters (Barkai & McQuaid, 1988).[2] Another example of surprise comes from a species

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[2] The horrifying aspect was the speed with which the whelks consumed their erstwhile predators: about 1,000 lobsters were completely annihilated within 45 minutes (Wilcox, 2018).

of butterfly that lays its eggs in a particular host plant (Singer & Parmesan, 2018). An invasive plant outcompeted the butterfly's native host, but the butterfly adapted to the invader. Around twenty years later, the invader was eradicated, but the butterfly could not switch back to its original host and went locally extinct. A third example comes from interactions between plants and soil microbes, which have been known to reverse, changing from positive to negative feedback (Casper & Castelli, 2007; Klironomos, 2002; see also Section 2.2). Finally, Benincà et al. (2008) observed unexpected and significant changes in species abundances and community structure in an experiment on a plankton community isolated from the Baltic Sea, even though the experiment was conducted in a controlled laboratory setting with most conditions kept constant.

The frequency of surprises like these in ecology has been documented. Doak and colleagues (2008) conducted a survey and found that surprises are far from rare. They outlined at least sixteen cases of famous surprises just within the subfields of population and community dynamics and reported that 98 per cent of established field ecologists affirmed that they had encountered surprise events akin to the sixteen cases. Moreover, many of the respondents revealed that the majority of surprising results had not been subsequently sent for publication, 'the implication being that these observations were uninteresting, bothersome, embarrassing, or not sufficiently well chronicled and understood through proper application of the scientific method, and thus were *underreported* in the scientific literature' (p. 956, my emphasis).

But what does the existence and frequency of surprises mean for ecological research? In the philosophical literature, a few surprises are viewed as a positive and integral aspect of scientific practice. Scientists learn from surprises, as understanding why they occur leads to scientific progress (Morgan, 2005; Parke, 2014). However, too many surprises are problematic. In the above examples, the scientists had identified patterns in nature (or the laboratory) and formulated expectations based on those patterns. Yet these patterns were ephemeral: they existed for a while, but at some point, they ceased, resulting in surprise. This explains why surprises are problematic: scientists rely on identifying patterns to generate generalisations, on which they base explanations, predictions and interventions. A surprise indicates that the explanation, prediction or intervention has failed or is likely to fail.

Ecological complexity (which includes the notion of causal heterogeneity) explains both the frequency and magnitude of surprises in ecology. Ecological phenomena have numerous, diverse and variable causes, so the behaviour of ecological systems does not always go as expected. This diversity and variability is the reason why the patterns that scientists detect are likely to be ephemeral, resulting in surprise. Nonetheless, as we shall see in the next section, there is

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a view which states that frequent surprises only occur in disciplines that are immature or whose theories or methods are somehow flawed (Doak et al., 2008; Hitchcock & Sober, 2004).

1.2 The Scientific Status of Ecology

Some ecologists believe that the frequency of surprises in their discipline should be taken as an indication that there are gaps in our knowledge of ecological systems. In some sense, worrying about the quality of a discipline's research is something that all scientists (ought to) do, as it helps to maintain standards and improve methods in scientific practice (Hitchcock & Sober 2004).[3] However, there are ecologists who go much further, questioning whether ecology should be considered a science at all, or lamenting that it is at best a 'soft' science. Ecologists are often said to suffer from 'physics envy', wishing that their theories, methods and results would more closely emulate those in physics (Egler, 1986; Kingsland, 1995 p. 234; McIntosh, 1987; Shrader-Frechette & McCoy, 1993 p. 34). Another phrase sometimes invoked is that of 'stamp collecting', which is the lot of scientific endeavours that are merely descriptive, lacking general theories, predictive power and the ability to be expressed mathematically (Johnson, 2007; Kingsland, 1995 p. 200). As historian Sharon Kingsland points out, the introduction of mathematical models into ecology was viewed by ecologists themselves as an important step towards the discipline becoming a real science, and that this trend is ongoing, as 'ecologists continue to look towards mathematics and the physical sciences for ideas, techniques and models of what science should be' (1995, p. 234).

Despite these 'advances', there is a small but persistent and vocal group of ecologists who continue to worry. Every few years publications appear, often in monographs or the opinion section of major journals, expressing misgivings about the scientific status of ecology or one of its sub-disciplines. Perhaps the most famous of these critiques is Peters's aptly titled *Critique for Ecology* (1991), which criticised ecologists for not providing testable hypotheses in the form of precise predictions. Moreover, Peters argued that theory did not play a significant enough role in ecological research as it did little more than provide the conceptual inspiration for a scientific investigation. It seems that many ecologists took this criticism to heart, as 'across the western world there were professors who removed the book from library shelves to prevent their students from reading it, lest they became demotivated' (Grace, 2019). A more recent version of this view appears in Marquet et al. (2014), who argue that ecology does not have enough 'efficient theories', by which they mean theories

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[3] I thank Jack Justus for pointing this out.

that ‘are grounded in first principles, are usually expressed in the language of mathematics, make few assumptions and generate a large number of predictions’ (p. 701). On a similar note, Houlahan et al. (2017), argue that ecology has ‘abandoned prediction [and] therefore the ability to demonstrate understanding’ (p. 1). Moreover, it is still an ‘immature discipline . . . [that] must move beyond such qualitative coarse predictions to riskier, more quantitative, precise predictions, sensu Popper’(p. 5).

There are also critiques of sub-disciplines or types of research, which are in some sense more alarming, as they could be used by universities or funding bodies to limit the amounts allocated to those disciplines or methods. For example, Valéry et al. (2013) argued that their inability to find a process or mechanism specific to invasion biology ‘eliminates any justification for the autonomy of invasion biology’ (p. 1145). Courchamp et al. (2015) state that ‘one of the central objectives and achievements of fundamental ecology is to develop and test general theory in ecology’ (p. 9). Here, fundamental, or ‘pure’ ecology is contrasted to ‘applied’ ecology, which is aimed at solving particular problems and/or intervening on the world. The authors worry that applied ecology has seen an increase in support (economic and otherwise) in recent years, at the expense of fundamental ecology, which should be reversed (Courchamp et al., 2015).

Though it is primarily ecologists who worry about the scientific status of their field, these ideas are rooted in philosophy of science. As stated above, the ability to generate laws and the ability to make precise and accurate predictions used to be seen as *the* hallmarks of true scientific disciplines (Hempel & Oppenheim, 1948; W. C. Salmon, 2006). A discipline that could not provide either, would traditionally be considered at best ‘immature’ and at worst ‘soft’ or ‘unscientific’ (Rosenberg, 1989; see discussion in Winther, 2011). The more extreme versions of the positions are nowadays viewed as outdated in philosophical circles, yet aspects of them are still deemed important. Many philosophers arguing for a revised notion of laws, do so partly in order to show that sciences like biology are on a par with other sciences. For example, Linquist et al. (2016) argue that as ecology has resilient generalisations which ought to count as laws, this ‘should help to establish community ecology as a generality-seeking science as opposed to a science of case studies’ (p. 119).

Thus, there seems to be a general worry that ecology is far from an ideal science. The suggestions for how to improve the quality of ecological research vary: some argue that the answer is to find more or better laws, others argue for more focus on explanations or predictions, others still argue for more integration between sub-disciplines, and so on. My view is different, as I do not believe that there is anything, in principle, wrong with ecological research, merely that ecological research is particularly difficult in certain ways. These difficulties stem from the particular way in which ecological systems are complex.

1.3 Outline

My aims, in this Element, are to show that (i) our current views about complexity do not capture how complexity works in ecological systems (ii) we should reconceptualise complexity to include causal heterogeneity (iii) this reconceptualisation explains some of the important difficulties that ecologists face and (iv) this reconceptualisation can point to some ways of mitigating these difficulties. The argument will proceed as follows. In Section 2, I examine the concept of 'complexity' in ecology. I start by providing a brief sketch of the main characteristics associated with complexity and then move to an in-depth account of some of these characteristics, that is, those that affect the study of ecological systems. I then turn to Levins's (1966) account of complexity and trade-offs between model desiderata, which I subsequently extend and refine. In Section 3, I examine some of these trade-offs in more detail, showing how causal heterogeneity creates difficulties for generalisations, predictions and interventions. In Section 4, I argue that this explains but does not justify the worry that ecology is not a true or sufficiently mature science. I show that even if we give up on extensive generalisation in ecology, ecologists are capable of making successful predictions and interventions. Rather than being embarrassed by the modesty of ecological generalisations, ecologists and philosophers should recognise the scientific and practical value of ecology's methodological toolkit. In Section 5, I outline some concluding remarks on generalisation and prediction in science more broadly.

This Element is not just meant for a philosophical audience. I hope that any ecologists looking for an alternative philosophical view of science, that accounts for the peculiarities and idiosyncrasies of their discipline, will find the arguments I present helpful. Moreover, I hope that this philosophical approach can be used by practicing scientists to support the alternative, undervalued research strategies examined in Section 4. Finally, this discussion of ecological complexity could also be helpful for scientists in other disciplines whose systems are also causally heterogeneous, such as Economics or Climate Science.

2 What Is Ecological Complexity?

The claim that ecological systems are complex is uncontroversial. Simon Levin's declaration that ecosystems are 'prototypical examples of complex adaptive systems' (Levin, 1998) is frequently taken as the starting point for discussions of complexity in ecology (Parrott, 2010; Proctor & Larson, 2005; Storch & Gaston, 2004). Nonetheless, there is no simple answer to the question, ‘what is ecological complexity?’ as there is no single, universally accepted definition of ecological complexity. Instead, there are a number of diverse and not always overlapping characterisations originating in various disciplines, including biology, physics and social science (Bascompte & Solé, 1995; Donohue et al., 2016; Levin, 2005; Shrader-Frechette & McCoy, 1993; Storch & Gaston, 2004).

As there is no short answer to the complexity question and no comprehensive definition of the term, the aim of this section is to provide a guide for thinking about the question ‘what makes an ecological system complex?’ I will start with some background on the concept of complexity, as it was discussed within and outside ecology (Section 2.1). In Section 2.2, I will outline the most important characteristics of ecological complexity. In Section 2.3. I will examine the epistemic[4] implications of complexity, namely difficulties in generalising, predicting and intervening on ecological systems. In Sections 2.4 and 2.5, I will connect the discussions of the previous sections, arguing that in the context of epistemic difficulties, ecological complexity should be understood as the combination of ‘having multiple parts’, ‘interaction’ and ‘causal heterogeneity’.

2.1 Ecological Complexity in Context

Though aspects of complexity have been studied in various disciplines for more than 150 years, interest in complex systems began in earnest in the 1960s and 1970s, and gained momentum in the 1980s (Hooker, 2011; Miller & Page, 2009; Simon, 1962; Wimsatt, 1972). The subsequent explosion of research on complexity and its effects on a variety of phenomena, had important and long-lasting implications for scientific practice, as it contributed to the establishment of a framework for anti-reductionist philosophy of science (Hooker, 2011; Mitchell, 2009), along with the recognition that the emergence and manifestation of complexity, especially in biological systems, is an worthwhile and fruitful research topic (McShea & Brandon, 2010; Mitchell, 2009; Wimsatt, 1972).

Despite – some might say because of – the level of interest and research in complex systems, a single, unified definition of complexity has yet to be agreed on (Hooker, 2011; Ladyman et al. 2013; Miller & Page, 2009). In lieu of a precise or formal definition of complexity, scientists and philosophers usually list some characteristics that tend to appear in complex systems. It is worth noting that there

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[4] For readers without a background in philosophy, the term ‘epistemic’ here means related to *knowledge*. I am interested in the effects of ecological complexity on what ecologists know about the systems they investigate, how they know it and what difficulties arise in the acquisition of this knowledge.

is quite a bit of overlap, as some characteristics appear frequently. One such characteristic is having ‘multiple interacting parts’, which seems to be a basic requirement of complexity. The idea is that a high number of parts and (dynamic) interactions between them increase the likelihood of complex behaviours. Table 1 contains a representative selection of characterisations of complexity, from complex systems science and (philosophy of) biology[5]. As we can see, multiple interacting parts (highlighted in bold), features prominently.

Within the discipline of ecology, the context of complexity has its own history. Here, discussions of complexity were originally related to a question that was considered fundamental, namely, ‘how are ecological systems possible?’ Early influential ecologists, such as Odum, Elton and MacArthur, found the ability of populations, communities and ecosystems to persist, in spite of internal and external disturbances, quite remarkable, hypothesising that this apparent stability was caused by the diversity and connectivity of ecological communities (Kingsland, 2005; McCann, 2000 Odenbaugh, 2011). The general idea is that complex communities are more able to adapt to changes, such as disturbances or perturbations (fires, new competitors/predators, sudden climatic changes), without falling apart. This view was famously disputed by Robert May (1973), who used mathematical models to show that we should expect complex communities to be less stable. Subsequent generations of ecologists have refined the concepts of diversity, complexity and stability in order to bolster their favoured side of the debate, while philosophers of ecology have provided their own clarifications and categorisations of the various views (McCann, 2000; Odenbaugh, 2011). A current consensus seems to be that complexity is indeed an inherent feature of healthy and mature ecological systems, even though such systems may be susceptible to particular disturbances (Hooper et al., 2005; Loreau et al., 2001; McCann, 2000; Parrott, 2010).

The brief outline of the context of ecological complexity highlights two important points for our discussion. First, it is uncontroversial, indeed quite common to consider multiple interacting parts as key features of complex systems, including biological systems. Thus, there is also no difficulty in recognising that it is also a key feature of complex ecological systems. Second, whether or not ecologists agree that complexity leads to stability, they seem to agree that complexity is an inherent feature of (at least healthy) ecosystems. This is an important theme that will appear throughout the Element: the complexity of ecological systems is an inherent feature of the systems themselves. In other words, it is inescapable.

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[5] The first five quotes on the table have been taken from a list in Ladyman et al (2013), who collected quotations from a 1999 special issue in *Science* on complex systems.