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Like Hercules and the Hydra: Trade-offs and strategies in ecological model-building and experimental design



S. Andrew Inkpen

Department of History and Philosophy of Science, University of Pittsburgh, 1017 Cathedral of Learning, 4200 Fifth Avenue, Pittsburgh, PA 15260, USA

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ABSTRACT

Experimental ecologists often invoke trade-offs to describe the constraints they encounter when choosing between alternative experimental designs, such as between laboratory, field, and natural experiments. In making these claims, they tend to rely on Richard Levins' analysis of trade-offs in theoretical model-building. But does Levins' framework apply to experiments? In this paper, I focus this question on one desideratum widely invoked in the modelling literature: generality. Using the case of generality, I assess whether Levins-style treatments of modelling provide workable resources for assessing trade-offs in experimental design. I argue that, of four strategies modellers employ to increase generality, only one may be unproblematically applied to experimental design. Furthermore, modelling desiderata do not have obvious correlates in experimental design, and when we define these desiderata in a way that seem consistent with ecologists' usage, the trade-off framework falls apart. I conclude that a Levins-inspired framework for modelling does not provide the content for a similar approach to experimental practice; this does not, however, mean that it cannot provide the form.

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1. Introduction

Richard Levins famously argued that model-building in population biology requires confronting trade-offs among three desiderata: realism, generality, and precision (Levins, 1966; Palladino, 1991).¹ According to Levins, modellers can build models that maximize at most two of these desiderata; they may build models that are realistic and general, or precise and realistic, or general and precise, but not ones that are maximally precise, realistic and general. He called these three combinations of desiderata “strategies.” Because these strategies were associated with equally important but non-identical scientific aims (i.e., understanding, predicting, and modifying nature), Levins' analysis provided a rational framework for appreciating methodological pluralism in modelling. As he concluded, a “multiplicity of models” is “imposed” on us (Levins, 1966, p. 431). His arguments are now commonplace in philosophy of biology (Godfrey-Smith, 2006; Matthewson, 2011; Matthewson and Weisberg 2009; Orzack & Sober, 1993; Odenbaugh, 2003, 2005, 2006; Weisberg, 2006, 2013).

Levins' work seems to have also seeped into experimental ecology. Since the 1980s, ecologists have repeatedly considered experimental practice in terms of trade-offs. Experimentalists invoke trade-offs—sometimes Levins' very own—to describe the constraints they encounter when choosing between alternative experimental designs.² Ecologist Peter Morin has described a three-way trade-off in ecological experimentation between realism, precision, and generality (Morin, 1998). Nelson Hairston and others invoke Levins more loosely, describing their own work in terms of Levins-style trade-offs without committing to his specific terminology (Hairston, 1989a,b).³ And many follow Jared Diamond when he argues that understanding “trade-offs is essential to appropriate experimental design” (Diamond, 1986, p. 3).

The apparent ease with which Levins' framework has been appropriated for discussions of experiments has stymied efforts to

² Ecologists sometimes refer to “venues” in this context, rather than “designs.” Beyond what I cite in the text, see: Hairston, 1989a, p. 120, 1989b, p. 65; Peters, 1991, pp. 136–41; Morin, 1998, pp. 50–1, 2011, p. 59; Irschick & Reznick, 2009, p. 174; Karban & Huntzinger, 2006, pp.54–5; Skelly, 2002; Skelly & Kiesecker, 2001. See trade-off diagrams in Hairston, 1989a, p. 120 and Morin, 1998, p. 51. See also Hunt and Doyle (1984), for a discussion of how structuring research agendas in ecology around Richard Levins' trade-offs between realism, precision, and generality—discussed below—may help ecology make faster progress.

³ Experimental biologists also invoke Levins' notion of “robustness” (Diamond, 1983).

E-mail address: sai22@pitt.edu.

¹ This is the common interpretation of Levins' argument (Matthewson, 2011; Weisberg, 2006). Levins does not use the term “trade-off” in his 1966 article, but many others, including Levins himself at a later date, have discussed his argument in terms of trade-offs (Levins, 1993).

rigorously evaluate its ability to accurately capture experimental methodology. A number of questions remain for the philosopher interested in experimentation: What are the specific desiderata of experiments and how do they differ from Levins' model-building desiderata? In what ways, and for what reasons, do these desiderata trade-off against one another? How is this reflected in the "strategies" practiced by experimenters? Do such trade-offs "impose" methodological pluralism in experimental practice? This paper is a first step towards answering these questions. In accordance with the development of Levins' ideas in the recent modelling literature, I focus on the trade-off between "generality" and "precision," and evaluate whether this trade-off applies to experimental practice. To avoid unnecessary complexities, I confine my analysis to *theoretical* modelling, leaving *material* models aside.

This paper has four further sections. In Section 2, I engage with Michael Weisberg's recent work to describe what I mean by "generality" (Weisberg, 2013). In Section 3, I consider strategies modellers employ to increase generality, notable among these is the sacrifice of precision. Section 4 asks whether these strategies accurately capture the practices of experimenters in ecology. I argue that, of four strategies modellers employ to increase generality, only one may be unproblematically applied to experimental design. Furthermore, modelling desiderata do not have obvious correlates in experimental design, and when we define these desiderata in a way that seem consistent with ecologists' usage, the trade-off framework falls apart. Section 5 is a brief conclusion. This paper intervenes in recent philosophical debates about the practices of experimenting and modelling, but it also has implications for discussions in biology about experimental trade-offs.⁴

2. On generality

One fundamental similarity between theoretical modelling and experimenting is that they are both (often) instances of *indirect* or *surrogate* analysis: rather than investigating a natural system directly, one explores a stand-in that is often intentionally simplified and idealized (Baetu, forthcoming; Godfrey-Smith, 2006; Weisberg, 2007a).⁵ In the experimental literature this stand-in is typically called the *object of study* or just *object*; in the modelling literature, the *model*. For example, experimental ecologists sometimes investigate the effects of competition between organisms contained in laboratory bottles because, unlike natural systems,

such objects of study are small and easy to manipulate and monitor. As ecologist Nelson Hairston poetically reflects, "Ecological relationships are so complicated that in attempting to deal with them, we must, like Hercules fighting Hydra, put some of the heads under rocks while we contest with the others" (Hairston, 1989b, p. 55). Even where experiments are performed directly in a natural system (e.g., an island), this natural object of study is often intended as a stand-in for other, related natural systems.⁶ Ecological modellers similarly explore simplified models of competition, often described by mathematical equations, as stand-ins for competition in natural systems (Weisberg, 2007a).

The desiderata "generality" is a measure of the number of "targets" to which a model or experiment "applies." Targets are not themselves real-world phenomena, but *abstractions* over such phenomena. Looking at the same real-world phenomena, the Adriatic Sea for example, different groups of ecologists will abstract different targets: a community ecologist will be interested in the set of factors that influence community organization; a behavioural ecologist, the set of factors influencing the foraging behaviours of a particular species (Elliott-Graves, 2012; Weisberg, 2013, p. 90ff). In each case, different targets will be abstracted away from the total set of factors making up the Adriatic Sea. A model that applies to more targets than another is said to be more general. Likewise for experiments.

Although generality is in practice often hard to assess, it is an important desiderata of both experimenting and modelling (Cook & Campbell, 1979; Orzack & Sober, 1993). This is of course because researchers often want their analyses to apply beyond the stand-in studied—in fact this is very often the goal of their analysis. Furthermore, greater generality is closely linked to greater prediction, explanation, and scientific understanding, though in nontrivial ways in which I will not summarize here. Suffice it to say that generality is important and greater generality is normally a good thing.

We can subdivide generality into the logically *possible* targets to which a model or experiment applies and the *actual* targets to which a model or experiment applies. These we call *p-generality* and *a-generality* respectively. In this paper I will be concerned only with *a-generality*, in part because, in the words of Kenneth Waters, biologists "are much more interested in the actual than the possible" (2007, p. 577).⁷ For ease of diction, I will use "generality" throughout.

What does it mean for an experiment or model to "apply to" a number of targets? Although this is controversial philosophical terrain, for the purposes of this paper we can afford to keep the discussion at a fairly broad, informal level. In the case of modelling, many recent analyses treat generality as grounded in model-target similitude: the relevant respects and degrees (as judged by the individual modeller or their community) in which the model is similar to its intended targets (Parker, 2009; Weisberg, 2013). In other words, a claim about the generality of a modelling analysis is justified on the basis of an assessment of the many known similarities and differences between the properties of the model and those of its intended targets. Models that are similar (in the right ways) to many intended targets will be more general than models that are similar to only a few targets.

Since this approach to assessing generality depends on what a modeller, or their scientific community, *judges to be* a sufficient

⁴ Distinguishing between experimental practice and model-building is beyond the scope of this paper (see footnote 5). As working definitions, I agree with Parker (2009) about what constitutes an experiment: "An *experiment* can be characterized as an investigative activity that involves intervening on a system in order to see how properties of interest of the system change, if at all, in light of that intervention. An *intervention* is, roughly, an action intended to put a system into a particular state" (Parker, 2009, p. 487). And as a working definition of modelling, Weisberg's (2007a) account is useful to keep in mind for this paper: "the indirect theoretical investigation of a real world phenomenon using a model" (2007a, p. 209).

⁵ One might think that intervention or manipulation is the unique mark of experimenting, not modelling. While experiments do involve manipulation, so too do many cases of modelling. And this is not just metaphor; the concrete models and model organisms of recent modelling analyses are certainly examples of modelling that involves learning from manipulation. One might also think that experimenting and modelling delineate very different styles of scientific work—the former "observational," the latter "theoretical"—but recent philosophical analyses seem to blur any such line. Francesco Guala argues that both play the role of "mediating" between high-level theory and the world (2005, p. 212). Emily Parke suggests that no methodological or epistemic distinctions can in general be drawn between experiments and simulation models (2014, p. 517; see also Parker, 2009). And Michael Weisberg subsumes both model organism research and natural experiments under his broader modelling framework (2013, pp. 24–5). See also Morgan, 2012, Peschard and van Fraassen (2014), Wimsatt (2015), and Winther et al. (forthcoming).

⁶ I agree with Baetu (forthcoming) that this use of surrogate analysis in "basic" research, as opposed to clinical contexts, has been overlooked in the literature.

⁷ See Lewis and Belanger (2015) for an approach to defining generality more precisely. See Orzack (2012) for a critique of Matthewson and Weisberg (2009) on generality and precision.

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