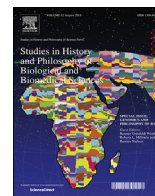




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The mind, the lab, and the field: Three kinds of populations in scientific practice



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ABSTRACT

Scientists use models to understand the natural world, and it is important not to conflate model and nature. As an illustration, we distinguish three different kinds of populations in studies of ecology and evolution: theoretical, laboratory, and natural populations, exemplified by the work of R. A. Fisher, Thomas Park, and David Lack, respectively. Biologists are rightly concerned with all three types of populations. We examine the interplay between these different kinds of populations, and their pertinent models, in three examples: the notion of “effective” population size, the work of Thomas Park on *Tribolium* populations, and model-based clustering algorithms such as *Structure*. Finally, we discuss ways to move safely between three distinct population types while avoiding confusing models and reality.

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What are the relationships among the populations that biologists postulate in idealized theoretical models, the populations they set up in experimental laboratories, and the populations they survey and sample in the wild? We describe three qualitatively different kinds of populations at the heart of distinct styles of scientific practice in ecology and evolution, viz., theoretical, laboratory, and field investigations. Distinguishing three types of populations—*theoretical*, *laboratory*, and *natural*—provides a useful lens for viewing both past and contemporary work in ecology and evolutionary biology.

Three examples illustrate the value of distinguishing theoretical, laboratory, and natural populations: the concept of “effective” population size, the work of Thomas Park on flour beetle populations, and the use of model-based genetic clustering algorithms such as *Structure*. In keeping with the “Genomics and Philosophy of Race” theme of the special issue in which this article appears, our

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trichotomy can assist analyses of the implications of genomic studies for claims about the existence (or the non-existence) of human races. In the conclusion, we suggest ways to avoid conflating the three kinds of populations. Researchers can cycle through natural, laboratory, and theoretical populations, expressing genuine interest in each population type. Theoretical, laboratory, and natural populations also pertain to fields beyond ecology and evolution, including statistics.

We analyze scientific practice. Although questions regarding realism and anti-realism, the concept–world relation, and the general ontology of science lurk, our trichotomy is not intended as a rubric for determining how much a model does or does not correspond to reality. Admittedly, an overarching aim of population biology is to understand the complex structure and dynamics of populations “in the wild.” Even so, the multiple ontologies of scientific practice are complex—arguably there is a world in a theoretical model (e.g., [Morgan, 2012](#)) or in an experimental system (e.g., [Leonelli, 2007](#)). Second, this article does not provide a singular, complete, and strict delimitation of the “population” concept. Other classifications and analyses of the concept are compatible with our view. We are pluralists about population concepts, about the kinds

of complex objects and processes one could delimit as populations, and even about distinct classifications of populations (e.g., Earnshaw-Whyte, 2012; Matthen & Ariew, 2002; Stegenga, 2010).

Our analysis side-steps explorations of the metaphysics of science and alternative classifications. We advocate “taking a look” (Hacking, 2007, 36–38) at styles of practice of working biologists. Which kinds of populations do biologists believe they are studying? Which figures in the history of biology might shine through as exemplars (Kuhn, 1970) of distinct styles of practice regarding populations? Which tools allow biologists to avoid conflating different kinds of populations and to perform important work internally, within each style of practice?

1. Three kinds of populations

Three kinds of populations used in the history and philosophy of population genetics, population biology, and evolutionary ecology can be distinguished: *theoretical*, *laboratory*, and *natural*.

1. *Theoretical populations* are groups of abstracted individuals (or genes) whose properties and behaviors are studied in formal models constructed with idealized assumptions.
2. *Laboratory populations* are collections of actual organisms—or parts of organisms, such as cell lines—assembled in an experimental setting.
3. *Natural populations* are collections of actual organisms living in the wild—settings that are not constructed expressly for studying the organisms. (But researchers might modify the habitat.)

Each of these kinds of populations is associated with its own kind of models, methods, and ontologies. Each can also be enriched by including stipulations about shared ancestry, proximity, or interactions between population members, such as competition, cooperation, or interbreeding. In practice, researchers may modify their use of the term “population” to suit the questions they pursue, which has two implications. First, elaborated definitions may not capture all appropriate uses of the three “population” concepts. For our purposes, only the minimal definitions in 1–3 above are needed. Second, populations are not exactly identical with the set of individual organisms composing them, whether in the mind or theory, the lab, or the field. The researcher also imposes the concept “population” onto organisms. Thus, although we describe the three kinds of populations as types of collections of objects, they might also be viewed as three distinct population concepts—in this way, laboratory and natural populations are also, in some sense, “theoretical.” Populations are abstractions even when their members are not. Differently put, scientists use the construct “population” to select specific attributes in which they are interested. These features are chosen because of particular goals, assumptions, and practices scientists bring to their objects of study in three contexts: the theorist’s mind, the experimenter’s labscape, and the field-worker’s landscape (Kohler, 2002). Paraphrasing the biologist Jean Rostand’s quip, “populations pass; the frogs remain.”

All three types of populations have received philosophical attention. Morrison (2000, 2002) shows which assumptions and idealizations were necessary to overcome conflicting notions of theoretical populations in the Biometrician–Mendelian debate in the early 20th century. We take work by Ankeny and Leonelli (2011) to be about laboratory populations, and contributions by Millstein

(2009, 2010) to be about natural populations.¹ Each type of population has a rich history of use in biology and originated in its own way (e.g., Kingsland, 1995; Kohler, 2002; Mitman, 1992). We side-step these histories and focus on one exemplary student of each kind of population: R. A. Fisher (theoretical), Thomas Park (laboratory), and David Lack (natural).

1.1. Fisher on theoretical populations

In the preface to the first edition of *The Genetical Theory of Natural Selection*, Fisher reflected on a remark by Arthur Eddington: “We need scarcely add that the contemplation in natural science of a wider domain than the actual leads to a far better understanding of the actual” (Eddington, 1929, 266–267; Fisher, 1930 (1958), viii). Fisher wholeheartedly agreed with Eddington. Fisher observed that practical biologists may deem it ludicrous to “work out the detailed consequences experienced by organisms having three or more sexes,” but this is precisely what they should do if they “wish to understand why the sexes are, in fact, always two” (Fisher, 1930 (1958), ix). Fisher recognized that:

ordinary mathematical procedure in dealing with any actual problem is, after abstracting what are believed to be the essential elements of the problem, to consider it as one of a system of possibilities infinitely wider than the actual, the essential relations of which may be apprehended by generalized reasoning, and subsumed in general formulae, which may be applied at will to any particular case considered. (Fisher, 1930 (1958), ix)

As Fisher understood, the creative power of mathematics lies partially in its capacity for generality, abstraction, and idealization. Very roughly, generality concerns the breadth of situations to which a mathematical structure applies; abstraction relates to the paucity of assumptions and axioms of the structure. The sparser the set of assumptions and axioms under which a theorem is derived, the more abstract it is (Cartwright, 1983). Idealization is reasoning about representations that may not be physically realized, such as infinitely long lines in geometry (e.g., Cartwright, 1989; Jones, 2005; Ohlsson & Lehtinen, 1997; Winther, 2014a). Mathematical activity involves *proofs* and *applications* of general, abstract, and idealized mathematical structures, deductively hitched (Hacking, 2014).

Fisher argued that certain properties of groups of organisms could be understood without detailed knowledge about individual organisms (Fisher & Stock, 1915). Specifically, Fisher considered the effects of selection in the aggregate, “borrow[ing] an illustration from the kinetic theory of gases” (Fisher & Stock, 1915, 60). Just as the statistical physicist studies the behavior of idealized gas particles in a theoretical aggregate, Fisher studied the behavior of abstracted and idealized organisms in a theoretical population, a theoretical aggregate that was “independent of particular knowledge about individuals” (Fisher & Stock, 1915, 61). In part through analogizing gas laws and selection laws, Fisher constructed a novel notion of population. Fisher’s analogy between physics and biology was deliberate and ongoing (Edwards, 1994, 2014; Morrison, 2000, 2002). By 1918, Fisher assumed that a population consisted of many “randomly mating” individuals,² each of which contained many independent genetic factors (Fisher, 1918, 401). In describing his later fundamental theorem of natural selection (FTNS), Fisher stipulated that “the [fundamental] theorem is exact only for

¹ In this issue, Millstein (2015) suggests that although her analysis of populations “is in the spirit” of natural populations, her analysis could also be applied to laboratory populations.

² We write “randomly mating” in quotes because the individuals in Fisher’s populations are abstractions and do not literally mate, although they do join their genetic factors randomly to give rise to the next generation.

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