

*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.

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 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., Matthen and Ariew 2002; Stegenga 2010; Earnshaw-Whyte 2012).

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?

2. 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 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 fieldworker’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., Mitman 1992; Kingsland 1995; Kohler 2002). We sidestep these histories and focus on one exemplary student of each kind of population: R.A. Fisher (theoretical), Thomas Park (laboratory), and David Lack (natural).

2.1. 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

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

wider domain than the actual leads to a far better understanding of the actual” (Eddington, 1929, 266-267; Fisher 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 1958 [1930], 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 1958 [1930], 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, and the more concrete cases it can subsume, perhaps incompletely (Cartwright 1983). Idealization is reasoning about representations that may not be physically realized, such as infinitely long lines in geometry (e.g., Cartwright 1989; Ohlsson and Lehtinen 1999; Jones 2005; 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 and 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 and 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” individuals², 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 idealized

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.

populations” (1958, 38). Just like “laws of gases” ensure averaged behavior across individual particles, so the FTNS ensures averaged behavior across individual organisms (1958 [1930], 39-40). As Morrison (2002) notes: “The idealised nature of the assumptions from that domain [statistical mechanics] served as a methodological model or analogy on which he based his own views about how to characterise a Mendelian population” (see also Morrison 2000, Chapter 7). Indeed, despite certain differences (e.g., the FTNS is not an irreversible law), both the second law of thermodynamics and the fundamental theorem of natural selection

are properties of populations, or aggregates, true irrespective of the nature of the units which compose them; both are statistical laws; each requires the constant increase of a measurable quantity... entropy of a physical system... [and] fitness... of a biological population. (Fisher 1958 [1930], 39)

Importantly, the biology-physics analogy pertained more to method than to content, involving particular mathematical approaches, approximations, and assumptions, especially the “averaging strategy” of abstracting and averaging across the properties and processes of individuals (the parts) to identify central tendencies of the population (the whole) (Sober and Lewontin 1982; Wade 1992; Sterelny and Kitcher 1998; Okasha 2004; Winther, Wade, and Dimond 2013).³ The FTNS and the analogy behind it show that general, abstracted, and idealized theoretical populations were Fisher’s object of study.

Later population-genetic theory has followed Fisher’s mathematical method of generalization, abstraction, and idealization.⁴ Fisher’s construction of theoretical populations in biology may also have informed the “population” concept he introduced to statistics. We return to this possibility in the conclusion.

2.2. Park on Laboratory Populations

The work of ecologist, evolutionary biologist, and entomologist Thomas Park illustrates the use of laboratory populations. Park spent much of his career at the University of Chicago developing, modifying, and observing the *Tribolium* flour beetle laboratory system. We examine his remarkable paper co-authored with Jerzy Neyman and Elizabeth Scott from the University of California, Berkeley (Neyman, Park, and Scott, 1956). Respecting the difficulties meeting the researcher studying “populations...in the field,” Neyman, Park, and Scott suggested two kinds of models that could substitute for fieldwork: “*mathematical* or *laboratory-experimental*” (1956, 42). Both kinds of models “depict

³ There are various ways to understand the FTNS (e.g., Frank and Slatkin 1992; Plutynski 2006; Okasha 2008; Ewens 2011; Edwards 1994, 2014). However, the power of Fisher’s overarching mathematical procedure is widely accepted.

⁴ Via his breeding experiments at Rothamsted Experimental Station (e.g., Fisher 1937; see Wade 1992; Winther, Wade, and Dimond 2013).

the workings of at least a part of nature” and, moreover, “enhance the interaction of certain factors” while diminishing or eliminating others (42). Most generally, both models are “abstractions of nature designed to illumine natural phenomena” (43). Since we have already explored mathematical theoretical populations, we set the first kind of model aside, focusing on laboratory populations.

In the first of two parts of the paper, “Biological Aspects,” written primarily by Park, “a laboratory-experimental model” is presented:

A population exhibiting a relatively rapid life cycle in a not too artificial laboratory habitat; cultured under easily controlled, yet manipulatory, environmental and trophic conditions; for which repeated censuses of all stages can be taken with negligible disturbance, and for which adequate replication is feasible. (Neyman, Scott, and Park 1956, 45)

This statement compresses a list of 10 characteristics that make a laboratory system optimal “for study of population phenomena.” *Tribolium* has many of the listed characteristics. Flour can easily be sieved to bring forth eggs, larvae, pupae and adults, facilitating censuses. Moreover, flour is simultaneously the “climactic,” trophic, and spatial habitat, simplifying a potentially complex environment. Finally, species can be mixed in the same flour, enabling studies of interspecific behavior. Park used *Tribolium* to study processes such as cannibalism, interference among individuals of the same and of different species, oviposition, predator-prey interactions, and host-parasite interactions (43) (Mitman 1992; Winther 2005). The influence of the *Tribolium* model continues through the work of Park’s students, including Monty B. Lloyd, David B. Mertz, Michael R. Nathanson, and Michael J. Wade.

Neyman, Park, and Scott worry that their laboratory model will be criticized as “artificial” (45). They accept that their model, though not simple, is simplified (45-6), but they reject the implication that artificial models are trivial. Laboratory populations are *abstract* compared with natural populations: many features of natural populations are eliminated in laboratory populations (e.g., rain, presence of predator species). Constructing a laboratory population is also an *idealization*: a previously nonexistent entity, the laboratory population, is granted reality in the counterfactual—or better yet, counternatural—experimental setting. Finally, the authors believe their model to be *general*, citing Park’s (1955) claim that the “unrealistic aspects” of laboratory models “may be a virtue instead of a vice,” and that such models “can contribute to the maturation of ecology, at least until... they are no longer needed” (Neyman, Park, Scott 1956, 46). Simplified, abstract, ideal, and general laboratory population models support some inferences about natural populations, with the caveat that laboratory and natural populations are not identical.

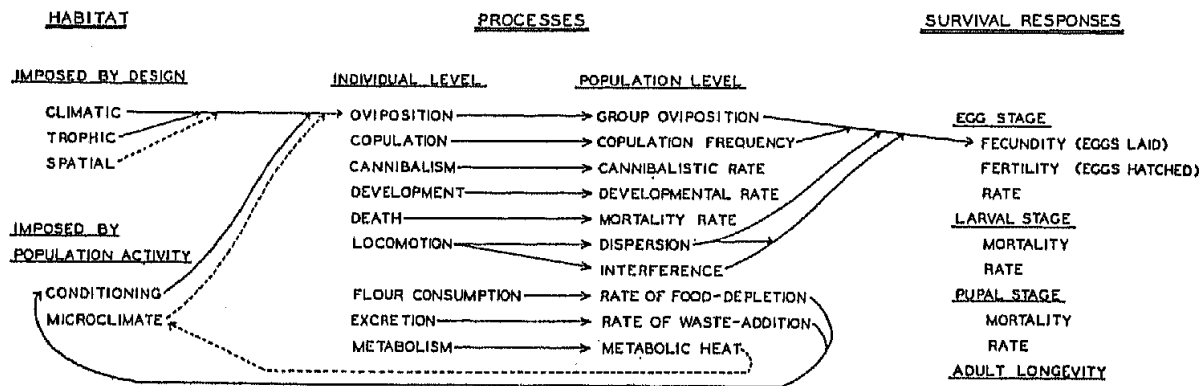


FIGURE 1

Major components of the *Tribolium* model. See discussion in text.

Figure 1. From Neyman, Park, and Scott (1956), 48.

The position of laboratory populations between theoretical and natural populations raises a question: Are laboratory populations models of natural populations or are laboratory populations themselves objects of further mechanistic or mathematical models? Put differently, are they representations or targets of other representations? Neyman, Park, and Scott think that laboratory models can “accelerate the understanding of *all* populations” (45), and represent, in many respects, natural populations. But they also hold that a laboratory population is itself a target of mathematical models (p. 59, ff.) and mechanistic models (Figure 1, 48), as we describe in Section 3.2 below. A laboratory population can also be a model for *another* laboratory population, potentially even of other species under distinct conditions.⁵ In short, laboratory populations are both representation and target.

Laboratory populations could be further compared with other “concrete models” such as “remnant models” in the museum (Griesemer 1990, 1991), “model organisms” (Ankeny and Leonelli 2011) or “compositional models” (Winther 2006b, 2011) in the laboratory, and “scale models” in engineering (Weisberg 2013). The main lesson for us is that laboratory populations represent natural populations imperfectly and serve as limited instantiations of theoretical populations.

2.3. Lack on Natural Populations

The ornithologist David Lack, known for studying Darwin’s finches in detail, was an early evolutionary ecologist and a student of natural populations. In the preface to the first edition (1983 [1947]) of his influential *Darwin’s Finches*, he sketched the nature of the book:

⁵ We thank Roberta Millstein for this point.

This is a work of natural history, based on a study of living birds in the Galapagos and of dead specimens in museums. The evidence is circumstantial, not experimental, so that theories must be presented cautiously. They should not, however, be excluded.
(p. xiii)

By studying natural populations, including remnant models stored in the museum (see Griesemer 1990, 1991)⁶, Lack was able to investigate plumage in the context of sexual selection, beak size differences among finches on different islands, and hybridization.

Natural populations are the basic unit of Lack's investigations. Lack circumscribes his populations using features of the Galapagos finches that interest him, viz., few competitors for food, few predators, and, crucially, "owing to geographical conditions," division into "a number of partly, but not completely, isolated populations, some of which are of very small size" (Lack, 1945, 115-116). Lack identifies natural populations using an important feature, geographical isolation.

Lack's units of study are natural populations, but similarly to our two other exemplars, Fisher and Park, his investigations draw on insights from other types of populations. Lack changed his theoretical interpretation but repeatedly referred to the same data from natural populations found in the field or stored in the museum. For example, in his earlier work, Lack (1945) hypothesized that most variation across populations was non-adaptive, attributable to the "Sewall Wright effect" (119, 135). By his 1947 book, in part due to Julian Huxley's influence, Lack's views changed significantly. He now postulated that interspecific competition fine-tuned the variation among populations, and species, of Darwin's finches. Cross-population variation was now understood as adaptive. Either way, Lack abstracted the properties of individuals from natural populations using data models including data tables, histograms, and maps.

Peter and Rosemary Grant took Lack's research program further, studying repeated bouts of selection in natural populations of Galapagos finches for over three decades. Discussing their precursor, in a review of a subsequent book by Lack, Peter Grant (1977) observed that "Lack himself was not a tester of ideas so much as an explainer of observations and hence a generator of ideas" and "Lack's field work strategy was to be a generalist, sacrificing some depth for breadth" (299). The Grants have maintained Lack's focus on natural populations, adding new insights about evolutionary, ecological,

⁶ We suggest that specimens in a museum are better thought of as samples, potentially un-representative, of natural populations rather than as constructed laboratory populations.

ethological, genetic, and physiological processes while remaining close to populations in the wild (Grant and Grant 1989; Weiner 2014 [1994]).

Many others have investigated natural populations. Among famous cases, consider the work by Theodosius Dobzhansky that “took him into the field and caused him to abandon his beloved *Drosophila melanogaster*, the standard fly, for a wild cousin, *D. pseudobscura*,” and that inspired historian Robert Kohler to write an entire book on the lab-field cultural border in biology (Kohler 2002, xiii). Or recall studies of variation in natural populations of the snail *Cepaea nemoralis*, in England (Cain and Sheppard 1950) and France (Lamotte 1959). Examples could be multiplied, as Endler (1986) does in a table presenting 140 “Direct Demonstrations of Natural Selection” (Table 5.1, 129-153). In all of this, natural populations are simultaneously assumed, abstracted, constructed, and investigated by those doing fieldwork and interested in natural processes.

| | Theoretical Population | Laboratory Population | Natural Population |
|------------------|--|--|--|
| Core definition | Groups of abstracted individuals (or genes) studied in formal models | Collections of actual organisms assembled in an experimental setting | Collections of actual organisms living in the wild |
| Worlds studied | All conceivable worlds | All materially possible worlds | Actual world |
| Article Examples | Wright-Fisher model populations | Park’s <i>Tribolium</i> | Darwin’s finches |

Table 1. Key contrasts among theoretical, laboratory, and natural populations.

To summarize, theoretical, laboratory, and natural populations are each important and can be distinguished (see Table 1). To say that these types of population can be distinguished is not to say that they cannot also be integrated. It is often necessary to invoke multiple types of population in the course of a single inquiry.

3. Reifying Populations

We now turn to three examples of the ways in which distinct types of population can be conflated, and ways of avoiding such confluations. First, as population geneticists since Sewall Wright have recognized, it would be a mistake to conflate the census size, N_c , of a natural population with its

“effective” population size. Second, we examine Neyman, Park, and Scott’s (1956) study of competition in two *Tribolium* species, indicating where there might be slippage between theoretical and laboratory populations, and why inferences from one to the other cannot be automatically justified. Finally, in turning to *Structure* analyses, we show how a tool that works perfectly well for identifying certain kinds of theoretical populations can fail to ground claims about natural populations.

3.1. Distinguishing Theoretical from Natural Populations via “effective population size”

A concept that is clarified by our distinction of theoretical, laboratory, and natural populations is “effective population size.” Effective population size highlights, in the semantics of the very term, translations that researchers must make between statements about natural and theoretical populations.

As evidenced by the example of Fisher detailed above, a century ago, evolutionary genetics was primarily a theoretical discipline. With little genetic data, evolutionary geneticists studied the ways in which evolution unfolds in theoretical populations (Haldane 1964). As more genetic data have become available, evolutionary genetics has become more empirical. Contemporary evolutionary geneticists study genome-wide data from both laboratory and natural populations. Evolutionary geneticists have thus needed methods for translating insights between their rich theoretical heritage and their current empirical genomic pursuits. Effective population size is one such bridging method.

Early evolutionary geneticists studied, and contemporary evolutionary geneticists still study, theoretical populations with properties such as the following (Hartl and Clark 1989; Hedrick 2005; Winther 2006a; Kliman, Sheehy, Schultz 2008; Ewens 2009; Nielsen and Slatkin 2013):

1. Mating is random.
2. The number of individuals that breed remains constant across generations.
3. The members of the population are hermaphroditic.
4. Every individual has the same expected reproductive success.

On the basis of her interests, the theorist might relax some of these assumptions or add other assumptions.⁷ The chosen assumptions lead to insights about the idealized theoretical populations. For example, the Wright-Fisher model starts from the assumptions in 1-4 and an additional assumption

⁷ When considering data, the researcher might be forced to add or relax assumptions because of the features of her data. For example, she might have data that rule out the possibility that mating is random with respect to traits she studies. Our focus in this paragraph and the next one is on theory rather than empirical work.

about the variance in offspring number among individuals. It ignores population structure, mutation, selection, two sexes, unequal numbers of breeding individuals across generations, and other non-idealized properties (e.g., Hartl and Clark 1989, 66 ff.; Gillespie 2004, 47 ff.; Ewens 2009, equation 35). Under the Wright-Fisher model, one can determine the rate at which genetic drift occurs. By adding more assumptions about mutation and selection, one can go further, determining, for example, the expected heterozygosity of the population (a measurement of genetic diversity) or the approximate probability that all individuals in the population will eventually carry a naturally selected allele.

The size of a theoretical population affects its evolution. For example, other things equal, the larger the Wright-Fisher population, the less the influence of drift, the greater the influence of selection, and the greater the expected heterozygosity. Early researchers also noticed that deviations from assumptions 1-4 can affect the evolution of a theoretical population in many of the same ways as can changing the size of the population. For example, modifying assumption 3 so that the population consists of different numbers of breeding females and males decreases the heterozygosity in the same way as decreasing the population size. Sewall Wright's (1931, 1938) effective population size, N_e , is one way of relating models of theoretical populations that include different assumptions. Whereas the census size, N_c , is the number of organisms in the population, whether in nature, the laboratory, or in theory, a population has effective size N_e if its genetic characteristics match a theoretical population meeting assumptions 1-4 with a census size equal to N_e . Differently put, the effective population size of a population is the size of an idealized population—specifically, a Wright-Fisher population—that would be expected to have a value of a statistic, or a theoretical property, identical to the one calculated or observed for the population of interest (e.g. Li 1955, 320-321; Crow and Kimura 1970, 110; Hartl and Clark 1989, 82; Hedrick 2005, 318, 319). One can choose different properties on which to base the correspondence of the two populations, leading to different effective population sizes. Ewens (2009) mentions variance, eigenvalue, and inbreeding effective population sizes, based on these three properties of theoretical population models. For example, the inbreeding effective population size of a population is the number of idealized individuals that, in a Wright-Fisher model, would generate the same level of inbreeding as measured in the natural population of interest.

When evolutionary geneticists study laboratory and natural populations empirically, they use the effective population size to relate natural and laboratory populations to theoretical populations. Because many natural populations do not meet the assumptions of theoretical models, the effective

population size is sometimes strikingly different from the census population size. For example, though the census population size of humans is over 7 billion, under most measures and models, the heterozygosity effective population size of humans is roughly 10,000 (Takahata 1993).⁸ The main reason for this discrepancy is the super-exponential growth in recent human history (e.g., Keinan and Clark 2012), possibly combined with a larger variance in offspring number in human populations than predicted by simple population models, such as the Wright-Fisher model.

Population geneticists are keenly aware that the simple theoretical models, such as the Wright-Fisher model, may be poor descriptions of natural populations. Nonetheless, the focus of much population-genetic research is to relate predictions from the theoretical populations to natural populations. Population geneticists fit theoretical population models to data from natural populations, thereby obtaining estimates of parameters such as migration rates, divergence times, and population sizes (e.g., Slatkin 1985; Neigel 1997; Beerli and Felsenstein 1999). One consequence of the use of the term “effective population size” is that population geneticists are reminded that the estimates of population sizes obtained should not be interpreted as the actual number of individuals in the natural population. Slatkin (1991) proposed an analogous usage of the term ‘effective migration rate’ for estimates of migration rates between populations.

We have already warned that conflating different types of populations leads to confusion. The concept of effective population size reminds evolutionary geneticists of distinctions between natural populations and different types of theoretical populations. These distinctions help population geneticists avoid reification errors among kinds of populations, but the effective population size itself can also be reified. Messer and Petrov (2013) argue that coalescent effective population size, which is sensitive to neutral evolution over long time scales, has been incorrectly used by some evolutionary geneticists as a single description of population size, leading some researchers to ignore the dynamics of natural selection in populations whose sizes fluctuate rapidly. The example of effective population size thus illustrates both the positive benefits of distinguishing theoretical, natural, and laboratory populations and the risks of not doing so.

3.2. Distinguishing Theoretical from Laboratory Populations in the *Tribolium* Model

⁸ This is not to suggest that the human population meets the assumptions of a Wright-Fisher model with a theoretical population size of 10,000. Rather, the empirically observed heterozygosity of humans is approximately the heterozygosity expected in a Wright-Fisher population of size 10,000.

When modeling a population, one necessarily ignores some aspects of the population in exchange for clarity about others. Neyman, Park, and Scott (1956) carefully articulated ways in which laboratory and theoretical populations of *Tribolium* inform one another. As we shall see, they found a strange experimental result. To investigate it, they constructed a mathematical model with unrealistic assumptions. Some of the assumptions of this theoretical model were empirically false, but false models may still be useful (Levins 1966, 1968): their broad conclusions may still be correct, and they may point to further experiments (e.g., Mertz, Cawthon, and Park 1976). In all of this, Neyman, Park, and Scott were careful to make their assumptions clear, and to distinguish two kinds of work and of populations – theoretical and laboratory.

A surprising laboratory result motivated the construction of a theoretical model. Isolated populations of *Tribolium confusum* and *Tribolium castaneum* were allowed to develop for 780 days in different, carefully controlled conditions, and their populations sizes were measured every thirty days. Because the beetles react differently to temperature and humidity, in some environments *T. confusum* became more numerous than *T. castaneum*, and vice-versa. In a parallel set of experiments, the two species were placed together in the same range of environments. In these experiments with interacting populations, one species of beetle was always eliminated. The counterintuitive result is that at a particular temperature and humidity, the species that was most prolific on its own was not necessarily the one that tended to prevail in competition. This consequence is surprising because it belies the expectation that some single intrinsic property (e.g., “vigor”) determines a high number of individuals in a particular environment, regardless of whether the species is alone or interacting with others.

As described in Neyman, Park, and Scott (1956, 59-74), the theoretical population retains only a few attributes of the original population:

1. Beetles have only one sex, there is no inter-specific variability in “voracity.”
2. There are only two life cycle stages (edible egg and voracious adult).
3. There is no spatial structure.
4. *Tribolium* activities (egg-laying, eating, and dying) are assumed to occur according to a Markov process.

This model's constrained notion of "population" offers the advantage of mathematical tractability at the cost of further divorce from natural populations. In exchange for these simplifications, mathematical machinery produces the following insights about theoretical populations:

1. The equilibrium population size in a single species is a tradeoff between voracity (egg eating) on one hand, and egg-laying and hatching time on the other.
2. In competition between multiple species, a species with a lower equilibrium population may still dominate a species with a higher equilibrium population if the former has a high enough voracity relative to the latter.

Having described and analyzed their new, theoretical population to come to these conclusions, they subjected some of the model's details to empirical scrutiny.

The assumptions of the theoretical model turned out to be inconsistent with more detailed experiments. Specifically, under the theoretical model, the number of eggs at a given point in time depends only on the *product* of the number of beetles and the amount of time that has passed. Ten beetles should produce the same number of eggs in five hours as five beetles in ten hours. Figure 8 of Neyman, Park, and Scott (1956, 73) shows that this is not so in the laboratory population: when time is varied but the number of beetles is kept fixed, variation in egg production is described by a line; in contrast, when the number of beetles is varied and time is fixed, variation in egg production is described by an exponential curve. The mathematical model is too simple. The theoretical and laboratory populations do not completely coincide. Indeed, the final section of Neyman, Park, and Scott (1956) describes failed attempts to make more complicated theoretical models accommodating the contrary data. Critically, this paper makes the assumptions clear in part by permitting the reader to consciously move between levels of abstraction—natural population to laboratory, and laboratory population to theoretical—always aware of what assumptions have been made and what information has been lost.

3.3. How to Avoid Conflating Theoretical with Natural Populations in *Structure* Analyses

We turn to another setting in which different kinds of populations can be conflated. In the past 15 years, population geneticists have used model-based clustering methods to assign individual organisms to distinct statistical clusters using genetic data (e.g., Pritchard, Stephens, and Donnelly 2000; Falush et al 2003, 2007; Tang et al. 2006; Hubisz et al 2009; Brisbin 2010; Maples et al. 2013). The most influential algorithm for genetic clustering is *Structure* (e.g. Pritchard, Stephens, and Donnelly 2000; Falush et al 2003, 2007). *Structure* analyses have been useful in understanding human genetic variation, especially as an exploratory tool for describing patterns of genetic diversity (e.g. Rosenberg et al. 2002;

Friedlaender et al. 2008). At the same time, their use has been controversial. Proponents of biological race concepts have argued that the classifications resulting from *Structure* analyses on human data mimic traditional race classifications and thereby validate a biological race concept, and biological realism about race (Sesardić 2013, Wade 2014; a careful defense of a biological race concept can be found in Spencer 2012, 2013, 2014, 2015; but see Kaplan and Winther 2013, 2014).

How do *Structure* analyses fit into our trichotomy? In the original paper describing *Structure* (Pritchard, Stephens, and Donnelly 2000), the clusters that the algorithm produces are called “populations.” But what kind of populations are they? To answer the question, consider *Structure*’s input, model, and output. The input to *Structure* is genetic data. Pritchard, Stephens, and Donnelly (2000) use three examples: simulated data, data sampled from three geographically distinct groups of Taita Thrush, and data from African and European humans. Thus, the genetic data used by *Structure* might come from theoretical populations (e.g. simulations), laboratory populations (e.g. Whitely et al. 2011), or natural populations. *Structure* uses genetic data to *estimate* populations.⁹ That is, *Structure* estimates the population membership of each organism in the sample—organisms might be assigned to more than one population—and estimates the allele frequencies in each population at each genetic locus in the dataset. To make these estimates, *Structure* compares the data provided to a model. In the model, individual organisms have only two properties—population memberships, which may be fractional, and genotypes. Populations, in turn, have only two properties—allele frequencies and Hardy-Weinberg equilibrium (HWE).¹⁰ Roughly, *Structure* finds population memberships and allele frequencies that lead to the closest fit between the model and the provided data.

In light of our trichotomy, then, *Structure* clusters are estimates of theoretical populations—they are the groupings that optimize the fit between a model of a theoretical population and data, which may come from theoretical, laboratory, or natural populations. Pritchard, Stephens, and Donnelly (2000) talk about *Structure* in similar terms in their original paper, and the distinction between estimates and theoretical quantities is fundamental to statistics (e.g., Wasserman, 2004, page ix, Figure 1; Fisher 1922, see below).

⁹ In our usage, the term “population” can apply to groups at different levels of a nested structure. Thus we call the targets of estimation in a *Structure* analysis “populations” rather than “subpopulations,” even though they may be subsets of a larger population.

¹⁰ The assumption of HWE can be relaxed; see Gao et al. 2007.

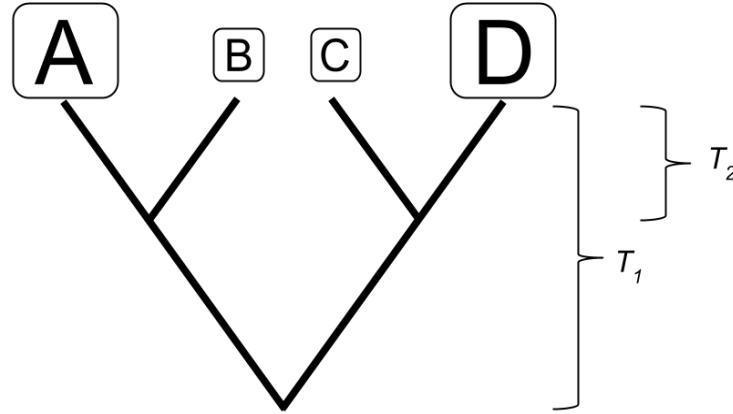


Figure 2. Four populations, *A*, *B*, *C*, and *D*, with their true history.

Treating clusters from a *Structure* analysis as populations with properties that are not part of *Structure*'s model can lead to inferential errors (Anderson and Dunham 2008; Weiss and Long 2009; Gilbert et al. 2012; Winther and Kaplan 2013; Putnam and Carbone 2014; Winther 2014b). Consider four (theoretical) populations with a true history depicted in Figure 2. Assume the populations undergo genetic drift but are not subject to natural selection (see e.g., Crow and Kimura 1970, Chapter 8; Hartl and Clark 1989, Chapter 2; Nielsen and Slatkin 2013, Chapter 2). Also imagine that populations *A* and *D* and their ancestral populations are very large compared with their divergence time in generations, T_1 . Because allele frequencies in large populations drift very slowly, allele frequencies will be similar in populations *A* and *D*. However, if populations *B* and *C* are smaller, with sizes similar to their divergence times, T_2 , from populations *A* and *D*, then the allele frequencies in populations *B* and *C* will change appreciably due to drift.



Figure 3. The results of *Structure* clustering by allele frequency.

In this example, populations *A* and *D* will have similar allele frequencies, but populations *B* and *C* will have distinct allele frequencies across the genome. A *Structure* analysis assuming three clusters ($K = 3$) would likely infer the three clusters as $\{A+D, B, C\}$ (Figure 3). No inferential errors have been made yet—this is the correct clustering when one considers allele frequencies alone. However,

depending on one's interests, it may make little sense to interpret cluster $\{A+D\}$ as a population that does not include B and C. For example, if the researcher is interested in questions about which groups of organisms freely interbreed, then the *Structure* clusters do not correspond with the researcher's purposes—A and D do not freely interbreed and have not done so for a long time. Shared ancestry is a fundamental component of biological taxonomy, but *Structure* does not directly inform about shared ancestry.¹¹

Even if the researcher is interested in exactly the type of groupings that *Structure* finds in data, reifying *Structure* clusters can still create problems. *Structure* analyses find a clustering scheme in which individuals in the same cluster have maximally similar genotypes and individuals in different clusters have maximally different genotypes. Suppose that we were to perform a *Structure* analysis on data from populations B and C in the example above, excluding populations A and D. With enough genetic data, *Structure* would likely be able to distinguish between populations B and C. But *Structure*'s assignments will be imperfect, and to the extent that *Structure* errs, it will tend to err systematically, assigning “B-like” individuals from population C partial membership in population B and assigning “C-like” individuals from population B partial membership in population C. Thus, the *Structure* clusters corresponding to populations B and C will likely be *more* genetically differentiated than the natural populations themselves. Estimates of population parameters, such as divergence times or migration rates, may thereby be prone to overestimating genetic differentiation when *Structure*-inferred clusters are treated as populations. If properties of *Structure* clusters are analyzed as if they were properties of natural populations, as is sometimes done (e.g. Jeong et al. 2014), then this potential bias must be kept in mind.

In all of this, the statistical methodology cannot be faulted. It has done just what we asked: produce groupings maximizing the fit between data and a model of populations as groups that meet HWE and have differing allele frequencies. If the user's purposes extend beyond the minimal population concept expressed by the model underlying *Structure*, then the user indeed has more work to do after running the analysis—supporting information is needed to make a case that a *Structure* cluster corresponds to the type of entity in which the investigator is interested. Users who imbue *Structure* clusters with characteristics that are not part of *Structure*'s model without such supporting evidence will make confused interpretations, especially vis-à-vis ecology and history.¹² Weiss and Long

¹¹ Kalinowski 2010 reaches a similar conclusion.

¹² Putnam and Carbone 2014 consider similar issues from a more technical point of view.

(2009) write that “architects of *structure*... are well aware of the limitations of the method and state them clearly in their papers [citations suppressed]. However, applications of such programs are often made without heeding caveats or recognizing the limitations of the underlying models with respect to the questions and data at hand.” (704) Weiss and Long are concerned with scientists reifying the output of *Structure* and similar programs, and they give examples of such reifications. Similar errors can occur when the media report on *Structure* analyses. For example, science journalist Nicholas Wade (2014, 100) describes a *Structure* analysis by Tishkoff et al. (2009) as revealing “14 different ancestral groups.” Our hypothetical example above points to one way in which a *Structure*-inferred cluster might not even approximately represent an “ancestral group” – these two kinds of theoretical populations should not be conflated.

In these cases, philosophical reflection might benefit scientific practice by demanding clarity about the aims and nature of the study, the kind of population(s) used in the study, and which inferences the populations used can legitimately support. Philosophical attention could prevent the inappropriate use of methods for questions they were not designed to answer. Keeping in mind our trichotomy of population types is not the only way to draw attention to these issues and avoid reification errors, but it is one way.

In this section, we have considered three examples of biological practice in light of our distinction between theoretical, natural, and laboratory populations. We viewed the effective population size, N_e , as a bridge between theoretical and natural populations, with the word “effective” serving as a helpful reminder that such a bridge is being crossed. Thomas Park’s work on *Tribolium* was a case study in the successful use of multiple types of population in the same line of inquiry. Park and his collaborators, Neyman and Scott, made their assumptions explicit each time they used a new type of population. We also saw that distinguishing theoretical, laboratory, and natural populations can help researchers avoid incorrect inferences when interpreting model-based genetic clustering results.

4. Conclusion

The main thrust of this paper has been to distinguish three kinds of populations—theoretical, laboratory, and natural. We have focused on scientific practice and have side-stepped several philosophical concerns, including realism and anti-realism, the concept-world relation, and the general ontology of science. In concluding, we mention three ways in which our analysis is related to larger themes in philosophy of science, and briefly consider the application of our trichotomy to statistics.

First, we are not committed to any particular ontological position about populations. Populations have been considered from realist (e.g. Millstein 2009, 2010, 2015), and pragmatic (e.g. Gannett 2003) perspectives. To our knowledge, no fictionalist account of populations has been offered (for fictionalism see Godfrey-Smith 2009a; Frigg 2010; Toon 2010; cf. Weisberg 2013). Our trichotomy might fit comfortably in such a fictionalist account. Theoretical populations could be viewed as fictional objects, worthy of study for their own sake, despite their imperfect correspondence with objects in nature, viz., natural populations. Laboratory populations might be seen as having characteristics of both fictional and material objects. Our analysis of scientific practice is potentially consistent with realist, pragmatic, and fictionalist ontological perspectives.

Second, our trichotomy can be viewed as a tool for *assumption archaeology*, the attempt to study the system of assumptions underlying a family of scientific models and theories (Godfrey-Smith 2009b; Servedio et al. 2014; Winther 2014b, under contract). Which kinds of assumptions are at play in modeling and theorizing, including methodological and ontological assumptions (Kuhn 1970; van Fraassen 1980; Levins and Lewontin 1985; Hacking 2002; Elwick 2012)? What are the functions of each assumption, and what happens when we replace a given assumption, or add new ones? What can occur when we forget that certain assumptions have been made? Many working scientists consider such questions carefully. We saw that Neyman, Park, and Scott analyzed their assumptions in an explicit and sustained manner, using a scheme similar to our trichotomy to understand their subject.¹³

Third, the concept of “population” in ecology and evolution is a potentially useful case study of model, concept, and ontology pluralism in science (Levins 1966, 1968, 2006; Dupré 1993; Cartwright 1999; Kitcher 2001; Longino 2002, 2013; Giere 2006; Winther 2006c, 2014a). At least sometimes, complex phenomena can be understood as involving multiple properties, objects, and processes, and can be viewed from several perspectives. For instance, Thomas Park interfaced theoretical and laboratory populations. Moreover, we can learn about one type of population without having to say something about another. For example, theoretical populations need not describe all aspects of natural populations in order to provide insight. Consider also that careful users of *Structure* compare *Structure* results with a plurality of kinds of evidence related to their interests and concerns.

¹³ Kaplan et al. 2015 effectively practice assumption archaeology in the “Gould on Morton” debate by carefully diagnosing the implicit questions and presuppositions at stake in this controversy.

We have focused on evolutionary biology and ecology, but our analysis of populations may be applicable to other fields. There is a historical reason for thinking this is so: one of the developers of the theoretical population concept in biology, R.A. Fisher, also contributed to the “population” concept in statistics.¹⁴ Fisher baptized the distinction in statistics between *population* and *sample*. Already in the first section of Fisher (1922), he faulted previous researchers for

apply[ing] the same name, *mean*, *standard deviation*, *correlation coefficient*, etc., both to the true value which we should like to know, but can only estimate [i.e., parameters or population moments], and to the particular value at which we happen to arrive by our methods of estimation [i.e., estimates or sample moments]. (1922, 311)

The population-sample distinction became fundamental to statistics. Fisher also states that statisticians proceed by “by constructing a hypothetical infinite population, of which the actual data are regarded as constituting a random sample¹⁵” (ibid). In addressing the basic problems of statistics (*specification*, *estimation*, and *distribution* 1922, 313), Fisher repeatedly appeals to infinite and hypothetical populations.

Are populations in statistics natural, laboratory, or theoretical? In their introductory textbook, Freedman, Pisani, and Purves define a statistical population as a class of individuals about which an investigator wants to generalize (1998, 333). When introducing students to statistical populations, some textbooks use natural populations as an illustration. For example, Whitlock and Schluter (2015) give examples of populations for use in data analysis, including “all the individuals of voting age in Australia,” and “all paradise flying snakes in Borneo” (4-5). Indeed, sometimes these groups are the targets of researchers’ interests: election analysts want to know how actual voters will vote. But to make inferences, statisticians invoke *theoretical* models of the populations in which they are interested. Sometimes the features of these models are tightly tethered to known features of the natural or laboratory populations under study, and sometimes the models contain features that are harder to verify. Either way, broad classes of statistical analyses—especially estimation and inference procedures—warrant claims about natural or laboratory populations to the extent that theoretical models reflect important features of the population of interest. There is a close analogy between this “statistical population” strategy and Fisher’s strategy in mathematical population genetics.

It is natural to see Fisher’s statistical population concept as an extension of his theoretical population concept. Individual elements are idealized, abstracted, generalized, and made

¹⁴ Similar statements could be made about Karl Pearson, as one of the anonymous reviewers of this manuscript pointed out.

¹⁵ On the history of “representative sampling,” see Kruskal and Mosteller 1980, replete with instructive diagrams for nine different meanings of the term. Interestingly, we have thus far been unable to find a history of the “population” concept in statistics.

interchangeable in exchange for the ability to make claims about the aggregate. Through Fisher's influence on statistics, theoretical populations—and questions about their relationship to natural and laboratory populations—exist in the inferential machinery of many fields across the natural and social sciences.

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