Chapter 3

The Concepts of Population and Metapopulation in Evolutionary Biology and Ecology

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Contemporary concepts of *population* in ecology and evolutionary biology vary greatly. Biologists rarely defend their choice of population concept and may not even explicitly characterize one. Of the explicit characterizations, some are extremely permissive, whereas others are much less so. Here are some examples to illustrate the diversity of meanings,[1] arranged from most permissive to least permissive:

- "A group of individuals of a single species" (Krebs 1985)
- "A somewhat arbitrary grouping of individuals of a species that is circumscribed according to the criteria of some specific study" (Orians 1973)
- "Group of organisms of the same species living in a particular geographic region" (Lane 1976)
- "All the members of a species that occupy a particular area at the same time" (Arms and Camp 1979)
- "Any group of organisms capable of interbreeding for the most part, and coexisting at the same time and in the same place" (Purves and Orians 1983)
- "A group of conspecific organisms that occupy a more or less well-defined geographic region and exhibit reproductive continuity from generation to generation; it is generally presumed that ecological and reproductive interactions are more frequent among these individuals than between them and members of other populations of the same species" (Futuyma 1986)

Most of the population concepts restrict populations to conspecific organisms; some include space and/or time as criteria, and some incorporate interbreeding or other interactions as criteria. In population genetics,

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[1] Most of these examples are taken from Wells and Richmond's (1995) longer list. As will be seen in this chapter, my own concept is closest to that of Futuyma's.

populations are generally characterized (again, assuming they are characterized at all) as a group of interbreeding organisms of the same species; sometimes "in a particular geographic area" (or the equivalent), is added.

Of the concepts listed, the permissive ones are the most problematic; if any grouping[2] of conspecific organisms could constitute a population, then populations could be gerrymandered, that is, their boundaries could be drawn so that the resulting "population" implied a favored conclusion. As I have argued elsewhere (Millstein 2009), if gerrymandered populations were legitimate populations, one could choose a grouping of conspecific individuals so that there was no variation in the trait in question (and thus, no selection or drift) or no fitness differences with respect to the trait in question (and thus, no selection). If gerrymandering were legitimate, then all resulting claims for the presence or absence of selection or drift would be equally correct. Yet, Darwin thought—and most contemporary biologists think—that selection can explain "the mutual relations of all organic beings to each other and to their physical conditions of life" (Darwin 1859, 1964: 80). It is hard to see how a selection process that was so description-relative (as the permissive concepts of population allow) could do any such thing.

More generally, different population and metapopulation delineations yield different answers about which ecological and evolutionary processes are occurring (more on this later in the chapter). Indeed, if populations and metapopulations are real biological entities (and not just human constructions), the wrong concept may cause *mischaracterizations* of ecological and evolutionary processes. As a consequence, inconsistent meanings of the terms population and metapopulation may lead to less than fruitful controversies in which the disputants are not genuinely disagreeing with each other, just using the same terms in different ways. Using the same terms with different meanings also makes it hard to compare results.

Another reason concepts of population and metapopulation are required is that evolutionary processes are often in flux. For example, selection can be operating in one season, and then not in the next, or it can be acting on different traits in different seasons. Thus, Godfrey-Smith's (2009) account of a Darwinian population (i.e., a population that has the conditions necessary for natural selection) needs to be supplemented with the prior notion of a population. Of course, the composition of populations also changes over time, with the addition of new members through birth and immigration and the loss of members through death and emigration. My point is that you cannot track changes in selection without identifying the entity (the population) within which those changes are occurring and that such changes can be too rapid for identification of a population by its selection processes. Indeed, the same population may be many "Darwinian

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[2] Following Gildenhuys (2009), I use the term grouping rather than group, since group has a technical meaning in evolutionary biology, as in group selection.

populations" over time, because there are different selection processes occurring over the course of a single year.

So, for all of these reasons, it is important to examine the concepts of population and metapopulation in ecology and evolutionary biology in order to find defensible concepts that avoid making ecological and evolutionary processes description-relative. But can a defensible concept be found?

This paper aims to illustrate one of the primary goals of the philosophy of biology—namely, the examination of central concepts in biological theory and practice—through an analysis of the concepts of population and metapopulation in evolutionary biology and ecology. I will first provide a brief background for my analysis, followed by a characterization of my proposed concepts: the causal interactionist concepts of population and metapopulation. I will then illustrate how the concepts apply to six cases that differ in their population structure; this analysis will also serve to flesh out and defend the concepts a bit more. Finally, I will respond to some possible questions that my analysis may have raised and then conclude briefly.

Background

By most accounts, the philosophy of biology is a young discipline that emerged out of the philosophy of science in the 1960s and 1970s.[3] It includes philosophical investigations into biological sciences such as ecology, molecular biology, developmental biology, cognitive ethology, and neuroscience in addition to evolutionary biology. The field has comparatively few textbooks, and articles appear in many different types of journals—philosophy of biology journals, history of biology journals, philosophy of science journals, biology journals, and combinations thereof—making it difficult to characterize. However, I think it is fair to say that much of the work in the philosophy of evolutionary biology, in particular, is captured by the title of a 1996 book by Robert Brandon: *Concepts and Methods in Evolutionary Biology*. In other words, there has been considerable effort devoted to clarification of central terms in evolutionary biology, including the concepts of fitness, species, adaptation, group selection, natural selection, and random drift, exemplified by Keller and Lloyd (1998) as well as considerable effort devoted to analyzing methods of empirical discovery, exemplified by Creath and Maienschein (2000). Both academic philosophers (i.e., scholars in philosophy departments) and biologists practice the philosophy of biology. Indeed, the field has been very much influenced by the philosophical work of biologists such as Michael Ghiselin, Stephen Jay Gould, Richard Lewontin, Ernst Mayr, and Michael J. Wade. Moreover, the best work in the

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[3] Byron (2007) provides a review of the standard history and an alternative one.

field has been done by those whose work pays careful attention to historical and contemporary biological practice.

Thus, it is surprising that there has been very little detailed analysis of a concept as central to evolutionary thinking as population, although there are notable exceptions (Goudge 1955; Wells and Richmond 1995; Camus and Lima 2002; Berryman 2002; Gannett 2003; Waples and Gaggiotti 2006; Pfeifer et al. 2007; Gildenhuys 2009). Metapopulation is also a widely used term (albeit one that is less central than population), and yet there has been a similar lack of analysis, again with notable exceptions (Hanski and Gilpin 1991; Harrison 1991; Hanski and Simberloff 1997). The fact that concepts as central as these have received such little philosophical attention contrasts with the massive literature on species concept. In 1969, David Hull remarked that: "the biological literature on the species concept is overwhelmingly large" (Hull 1969: 180), and it has increased significantly since then. Yet, the term population is arguably a far more central concept than species to the study of evolution. After all, populations are at the core of models in population genetics, ecological genetics, population biology, ecology, and evolutionary ecology. (Systematics is perhaps an exception in its use of species over population, but even systematists rely on populations in their analyses.) Populations must evolve before new species evolve; populations are constantly undergoing evolution, whereas the emergence of new species is a far less common event. Populations are also the entities within which abundance and distribution are studied. So, it is strange that the concept of population has received so much less attention. My goal in this paper is not to solve this sociological puzzle, but rather, to go some distance towards rectifying it.

There has also been relatively little written on the history of the concept of population in biology, although there are again notable exceptions (Gerson 1998; Winsor 2000; Gannett 2003; Hey 2009). As Hey describes, the biological use of the term arose out of its statistical use. In statistics, the term originally applied primarily to humans, referring to any set of individuals under investigation (e.g., human females over 50), whereas the biological use of the term refers to a "biological whole" composed of interbreeding individuals (more on this later in the chapter). Hey credits the transition from the statistical use to the biological use to thinkers such as Edward B. Poulton in 1903 (though Poulton does not use the term) and Karl Pearson in 1904. By 1939, biologists were using the term population in different ways, prompting Gilmour and Gregor to coin the term deme, meaning "any specified assemblage of taxonomically related individuals" (Gilmour and Gregor 1939: 333). Their intention was to distinguish between different types of demes. However, deme has come to refer to a collection of interbreeding organisms. Winsor (2000) reveals the irony of this usage as follows. Gilmour and Gregor originally intended the word gamodeme for this purpose, with topodeme and ecodeme referring to "demes occupying specified geographical areas and specified ecological habitats respectively"

(Gilmour and Gregor 1939: 333). However, this suggestion has largely been ignored, and it is simply the term deme that has stuck. Indeed, because the association between the term deme and interbreeding is so strong, and because I will be arguing for a broader term, I will avoid deme in favor of the more open-ended term population.

As for Darwin, one would be hard-pressed to find a contemporary characterization of natural selection that does not refer to changes in populations, and yet the word population does not appear in *The Origin of Species*. Darwin does use the term elsewhere, but primarily to apply to humans. The closest he comes to using the term population in *The Origin of Species* is when he refers to "individuals of the same species inhabiting the same confined locality" (Darwin 1859: 45), and claims that varieties generally arise locally (Darwin 1859: 298).

The history of the concept of metapopulation has been outlined, for example, by Hanski and Gilpin (1991) and Hastings and Harrison (1994). The term metapopulation—a population of local populations—was coined by Levins in 1970. However, Hastings and Harrison trace the general idea (albeit not the term) back to Nicholson and Bailey (1935). More commonly cited precursors for the idea include Wright (1940), as part of his shifting balance model, and Andrewartha and Birch (1954). Levins's metapopulation model is fairly specific; it refers to a population of local populations that go extinct and recolonize, with the local populations being equally spaced and of the same size (it is a deliberately simplified model). However, contemporary usage generally relaxes these strictures in a number of ways: as habitats have become increasingly fragmented as a result of human activities, the development of metapopulation models and their applications have increased in the last several decades. Metapopulation models vary, but at a minimum, most embody metapopulation concepts that allow for some degree of migration or dispersal among local populations. Clearly, however, any metapopulation concept will be parasitic on one's views concerning local populations.

The Causal Interactionist Population Concept

In discussing the concepts of population and metapopulation, my intended foci are evolutionary and ecological contexts, with the understanding that evolutionary factors affect ecological factors and vice versa (as the discipline of population biology recognizes), so that the two cannot be fully disentangled. Other disciplines, such as sociology, biomedicine, and statistics, also utilize population concepts, and perhaps it would be possible to provide a very general notion of population that would accommodate all disciplines. However, I suspect that the specific conceptions are the ones that are most relevant to the practice and understanding of evolution and ecology. In particular, my goal is to describe what are sometimes called lo-

cal populations of organisms[4] as well as groupings of local populations (i.e., metapopulations). By focusing on populations of *organisms*, I do not mean to deny that other biological entities, such as cells, also can form populations, but rather to suggest that the particular concept I will describe in this chapter would need modification before being used for biological entities other than organisms.

Elsewhere I defend the view that *populations are individuals* (Millstein 2009), drawing inspiration from the Ghiselin-Hull thesis that species are individuals (Ghiselin 1974, 1997; Hull 1976, 1978, 1980). It turns out that once one examines the criteria for individuality (e.g., being a spatiotemporally restricted entity), it is quite straightforward to demonstrate this otherwise oxymoronic-sounding thesis. The thesis that populations are individuals becomes even less controversial if one accepts the view that individuality comes in degrees—a point emphasized by Mishler and Brandon (1987) and others. For example, the key feature that distinguishes an individual from a mere set (which can be any arbitrary collection of individuals, such as the items on my desk) is that individuals are *integrated cohesive entities*.[5] Being an integrated cohesive entity implies that there are causal interactions among the parts of the individual, with the parts having a shared fate (so that what affects one part affects at least some of the other parts). For populations, the parts are organisms; for organisms, the parts are cells. Whatever you take the relevant causal interactions among organisms and cells to be, it will generally be the case that populations are not as integrated and cohesive as organisms are, which may simply mean that populations are not individuals to the same degree that organisms are.

However, for the purposes of this paper, nothing depends on the particular philosophical (or metaphysical) claim that populations are individuals. Indeed, the claim that populations are individuals can be understood equally well as a claim that populations are real entities that act (more or less) as a unit; they are *biological wholes*. Again, the key feature that makes something a biological whole is the presence of causal interactions among the parts. However, since many types of causal interactions exist, it is essential to specify which are the relevant causal interactions for the biological whole in question (Hamilton et al. 2009). Otherwise, the criterion is quite

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[4] For some species it is difficult to delineate one organism from another. This is an interesting complication that I hope to address in future work. The present analysis addresses only those species for which organisms are reasonably well delineated.

[5] Mishler and Brandon distinguish between integration and cohesion, using the former term "to refer to active interaction among the parts of an entity" and the latter term "to refer to situations where an entity behaves as a whole with respect to some process" such that "all the parts of the entity respond uniformly to some specific process" even if the parts are not interacting (Mishler and Brandon 1987: 400). However, I do not mean to imply this distinction here, and I think that *collective* would be a more appropriate term for what Mishler and Brandon call *cohesion*.

empty, especially if, for instance, infinitesimal gravitational forces count as causal interactions. In this chapter, I will argue that populations are integrated via the *survival and reproductive interactions of organisms*. In an earlier work, I show why other plausible candidates for causal interactions are not suitable (Millstein 2009). Here, I propose to defend my population concept differently, namely by showing its success in illuminating a number of cases and by demonstrating how it straightforwardly yields a metapopulation concept as well.

My proposed *causal interactionist population concept*[6] (with some additional clarifications that follow) is:

- *Populations* (in ecological and evolutionary contexts) consist of at least two conspecific organisms that, over the course of a generation, are *actually* engaged in survival or reproductive interactions, or both.
- The boundaries of the population are the largest grouping for which the rates of interaction are much higher within the grouping than outside (Simon 2002).

From these core ideas, it follows that organisms located in the same spatial area (including recent migrants) are part of the population *if and only if* they are interacting with other conspecifics. Furthermore, if a later grouping is causally connected by survival or reproductive interactions to an earlier grouping, then it is the same population; in this way, populations can be continuous through time.

Both survival and reproductive interactions cover a broad range of interactions.[7] *Reproductive interactions* include not just interbreeding (successful matings) but also unsuccessful matings. After all, unsuccessful matings can have important evolutionary and ecological consequences for the organisms that engage in them, especially if the organism never succeeds in mating. Offspring rearing activities (i.e., interactions between parents and interactions between parents and offspring) can also be included under reproductive interactions, since for many species the offspring produced will not survive without them.[8] As mentioned previously, some concepts of population include only interbreeding (if they include interactions at all); the suggestion here is that such concepts omit important factors relevant to ecology and evolution.

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[6] This presentation is slightly modified from the one in Millstein (2009).

[7] Social interactions might be a third category; however, my sense is that the social interactions that are relevant for ecology and evolution are those that involve either survival or reproduction (or both). Thus, social interactions will be included under those two categories.

[8] An anonymous reviewer suggests that offspring rearing activities ought to be viewed as survival interactions. While from the perspective of the offspring, these activities are survival interactions, from the perspective of the parents, they are reproductive interactions. Since both types of interactions are included as part of the concept, nothing turns on which way such activities are classified.

Ignoring survival interactions is equally mistaken. Survival interactions played a crucial role in Darwin's thinking; Chapter III of *The Origin of Species*, "Struggle for Existence," is focused almost entirely on them, with reproductive interactions receiving only the briefest mention.[9] Darwin states: "I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny"[10] (Darwin 1859: 62). In invoking this "large and metaphorical sense," Darwin provides a wide-ranging list of examples from which we can get a sense for the kind of survival interactions that organisms participate in. Eggs and seeds generally "struggle" the most; Darwin notes especially the seedlings that struggle to germinate in "ground already thickly stocked with other plants." More broadly, organisms can compete for "the same place or food" (i.e., "limited resources"), such that what is taken by one organism becomes unavailable for another. Organisms can also compete directly: "Two canine animals in a time of dearth, may be truly said to struggle with each other [for] which shall get food and live" (Darwin 1859: 62). But survival interactions in the struggle for existence need not involve direct or indirect competition; Darwin also discusses the possibility that "a plant could exist only where the conditions of its life were so favourable that many could exist together, and thus save each other from utter destruction" (Darwin 1859: 70). In other words, organisms of the same species can also "struggle together," or cooperate rather than compete. Again, the point is that survival interactions, such as those invoked by Darwin, are relevant to the cohesiveness of organism groupings and affect their ecological and evolutionary trajectories. Note also that even though asexual organisms do not engage in reproductive interactions per se, they do engage in survival interactions as described here. Thus, according to the

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[9] On a personal note, this is not a gratuitous reference to Darwin; on the contrary, teaching Chapter III for a philosophy of biology class was the source of my thinking that it was important to include survival interactions in the concept of population.

[10] The phrase "success in leaving progeny" is often quoted, but the frequency with which this sentence is quoted stands in stark contrast to the minuscule amount of space that Darwin used in discussing it. Perhaps, given the emphasis on survival interactions in the rest of the chapter, this passage might be better understood as referring to "success in producing offspring who survive." Indeed, Darwin subsequently remarks: "If an animal can in any way protect its own eggs or young, a small number may be produced, and yet the average stock be fully kept up; but if many eggs or young are destroyed, many must be produced, or the species will become extinct" (Darwin 1859: 66). In any case, "struggle for existence" is probably broader than "survival interactions," since some of the examples that Darwin discusses (e.g., a plant on the edge of the desert struggling for life against the drought) do not seem to involve interactions between organisms.

causal interactionist population concept, asexual organisms can be organized into populations, even multiple populations of the same species. (I will describe one such apparent case later in the paper.)

The causal interactionist population concept leaves out some criteria that other population concepts include. For example, it does not include space or time as a boundary; interactions influence the subsequent fate of the population (and thus, are what matter for ecology and evolution), regardless of whether they occur over large or small stretches of time or space. Indeed, if one were to delimit a grouping in space (a purported population) while excluding some organisms that were frequently interacting with members of the grouping, the predicted future trajectory of that grouping would be very misleading. Including organisms that are not interacting (drawing too large a spatial boundary) would be similarly misleading. For example, the presence of a new adaptive trait among the Torrey pines of San Diego is not likely to affect the Torrey pines of Santa Rosa Island, approximately 190 miles away; thus, one would be mistaken to predict the spread of the trait in Santa Rosa Island (which is not to deny that the trait could occur there, either through an unusual dispersal or a new mutation).[11] Time is excluded from my population concept for similar reasons: if over time, some descendents of earlier population members are no longer interacting with other descendents, it would be misleading to consider them together. Again, the point is that when organisms are interacting, their fates are (to some extent) linked, so that they form a biological whole.

The causal interactionist population concept also does not consider the amount of gene flow relative to selection; the concept of population needs to be independent of selection to avoid circularity, since selection takes place in populations and produces changes in populations. Migration is not included, either, primarily because it does not need to be; if an organism migrates out of the population, then it is no longer interacting with the other organisms. In contrast, if an organism migrates into the population and interacts, then it is part of the population; if it just "passes through," then it is not.[12] So again, interaction is the key criterion. Finally, the concept

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[11] The Wahlund effect demonstrates a similar point using a more theoretical approach. If two populations are completely isolated, the predicted genotype frequencies of the individual populations differ from that of the two populations pooled together. See, for example, Hartl and Clark's (1989) textbook for discussion.

[12] Slatkin (1987) notes that gene flow (as a result of migration with interbreeding) is difficult to measure and describes two types of measurement methods: direct and indirect. (The following discussion relies heavily on Slatkin's account, leaving out a great deal of the complexity; the reader is referred to Slatkin's excellent discussion for further details.) Direct methods use observations of the frequency and distance of dispersals, together with information about breeding success after dispersal, to infer the amount of gene flow between populations. Indirect methods use allele frequencies or DNA sequence differences with

does not include genetic relatedness, which merely tracks the outcomes of reproductive interactions rather than the interactions themselves.

Even though none of these candidate criteria (space, time, gene flow, migration, genetic relatedness) are included in the causal interactionist population concept, they all may be *indirect indicators* of (or proxies for) populations. This will be seen in the cases that follow.

The causal interactionist population concept also restricts members of the population to *organisms of the same species*. It is my impression that most concepts of local population do likewise. But more importantly, the term *community* can be used for multi-species groupings. Having different terms for each concept can better allow for the possibility of different dynamics in single-species groupings and multi-species groupings.

However, the causal interactionist population concept does not assume any *particular* species concept, excluding only those that define species in terms of populations (which would again introduce circularity). This position is partly to avoid entanglement in the seemingly endless debates over the concept of species, but also to allow for the possibility that there may be more than one legitimate species concept, as Mishler and Brandon (1987) and Ereshefsky (1992), among others, have argued. Thus, the causal interactionist population concept is neutral with respect to species concept; it has some similarities to Templeton's (1989) cohesion species concept, but is neither identical to nor reliant on it. Both Templeton's and my concepts focus on causal processes (or, in my population concept, interactions) rather

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population genetic models to estimate the level of gene flow that must have occurred to produce those patterns. Slatkin depicts two types of indirect methods. One method uses Wright's F_{ST} statistic to estimate the standardized variance in allele frequencies among local populations. The other method is Slatkin's own; it relies on the frequencies of rare alleles for its calculations. Both methods, according to Slatkin, can be used to estimate Nm, where N is the local effective population size (i.e., the number of breeding organisms in the population) and m is the average rate of immigration in an island model of population structure (where every local population is equally accessible from every other). To estimate m alone, an estimate of N from census data can be performed; N can be used as a measure of how strong drift is likely to be (smaller N = stronger drift). But the key thing to note is that all of these observations, measures, and inferences—dispersal, F_{ST}, N, m, drift—presuppose that the population structure is known. An assertion that dispersal is occurring presupposes that it is known that an organism is leaving one population and migrating to another. When allele frequencies or DNA sequences are sampled, a decision has to be made as to which organisms to sample from; a census of a population again presupposes that it is known which organisms belong and which do not. Thus, although these techniques may help determine population structure by serving as indirect indicators, population is the more basic concept. Population genetic methods do not replace the need to have a concept of population. (Thanks to Douglas Futuyma for encouraging me to clarify the relationship between population genetics approaches and the concept of population, although I am sure there is more to be said here.)

than outcomes, both incorporate a variety of causal processes not limited to reproductive (though not the same set), and both weigh the causal processes differently in different cases (see discussion later in the chapter). However, whereas the cohesion species concept incorporates *potential* processes (potential genetic exchangeability and potential demographic exchangeability), the causal interactionist population concept incorporates only *actual* processes (interactions). Moreover, whereas the cohesion species concept incorporates evolutionary processes, the causal interactionist population concept incorporates processes that give rise to evolutionary processes (e.g., struggle for existence), but not the evolutionary processes themselves.

The causal interactionist population straightforwardly implies a corresponding metapopulation concept.

Causal Interactionist Metapopulation Concept

The causal interactionist metapopulation concept consists of the following elements:

- *Metapopulations* consist of at least two local populations[13] of the same species, linked by migration or dispersal, such that organisms occasionally change which population they are a part of;[14] rates of interaction within local populations are much higher than the rates of interactions among local populations.

- If the rates of interaction within local groupings are *not* significantly higher than the rates of interaction among local groupings, it is a *patchy population*, a term coined by Harrison (1991).

As I mentioned briefly earlier, contemporary meanings of the term metapopulation are much less specific than Levins's meaning; the concept I propose is closer to the contemporary meaning. Migrations/dispersals form the basis of the interactions among local populations. Typically, these interactions are rare, but if they are nonexistent, there is no metapopulation—just a set of unconnected local populations. As these interactions are weak, a metapopulation is much less cohesive—much less a biological whole—than a local population.

As Hanski and Gilpin (1991) point out, the movement of organisms is different at different scales. The movements within a local population are routine feeding and breeding activities, whereas movements from one local population to another are "typically across habitat types which are not suitable for their feeding and breeding activities, and often with substantial risk of failing to locate another suitable habitat patch in which to settle" (Hanski and Gilpin 1991: 7). Thus, the interactions that bind populations together

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[13] As characterized in the previous section.

[14] As described in the previous section.

are different than the interactions that bind metapopulations. However, the following discussion will show that the types of interactions among the local populations of a metapopulation differ (some focused more on survival and others focused more on reproduction), which will require that the concept be elaborated a bit.

Six Case Studies

We will now turn to six case studies to illustrate the application of these concepts and to show their fruitfulness. Although other types of cases are possible, part of my intent is to demonstrate how the concept handles some seemingly problematic cases. All of these cases will draw upon the published results of particular biologists and will make inferences about population structure[15] based on those results. Thus, it follows that if their results are inaccurate, then my claims concerning the population structure are likely to be inaccurate as well—which is as it should be. Any claim that a particular grouping of organisms forms a particular population structure is an empirical claim, subject to being overturned by better data. The point is not to claim that any grouping of organisms definitely has a particular population structure, but rather to show what sort of population structure would be present if the results of the cited studies are accurate. Moreover, in each case I am not making a claim for the species as a whole (with the possible exception of *Eubalaena australis*), but rather for the species in particular places and at particular times—namely, the places and times of the referenced study. I take this approach not because I think that space and time are part of the population concept, but instead to acknowledge that a species may have one population structure in one place and time and a different population structure in a different place or time. In other words, a given population structure is not a permanent feature of a species, though particular species may tend to form certain types of population structures given their mating and feeding habits with respect to the characteristics of the habitats in which they live.

Case 1: One Continuous Population

Linanthus parryae (desert snow) is a well-studied flowering plant. Perhaps the most famous studies of *L. parryae* occurred in the Mojave Desert in the early 1940s by Epling, Dobzhansky, and Wright (Epling and Dobzhansky 1942; Wright 1943b). In years of heavy rainfall (which there were during this period), the swath of blue and white flowers is "almost like a carpet" (Provine 1986), spread over a large territory. In order to account for the evolution of species such as these, Wright (1943a) developed a "genetic

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[15] Here I am using the term *population structure* as a general term for the various ways that organisms might be organized: in one population, in several populations, in a metapopulation, or otherwise.

isolation by distance" model. According to Wright's model, when a species has limited mobility (as does *L. parryae*), the parents of any given individual come from a small surrounding region. Using his isolation by distance model, Wright (1943b) estimated that breeding group sizes were approximately one or two dozen productive individuals, with long-range dispersal being a rare event. The genetics of *L. parryae* were not known at that time; the numbers of blue and white flowers were sampled and counted at various locations under the assumption that the differences were genetic in origin.

Is this one population or many? The papers in question are not consistent on that point, sometimes referring to one population with groups, subgroups, or colonies, and sometimes referring to multiple populations. In a case such as this, one might be tempted to say that since there are groupings of interactions within the carpet (as a result of isolation by distance), it follows that there are multiple populations within the carpet. It certainly is not the case that every organism interacts with every other organism, and it would rarely be the case that every organism in *any* population interacted with every other organism. However, the carpet was an area about 80 miles long and on average 10.5 miles wide, with an estimated 10^{10}–10^{11} individual plants (Wright 1943b). It seems pretty clear that many of the plants were not interacting directly.

However, on the causal interactionist population concept, the boundaries of the population are the largest grouping where the rates of interaction are much higher within the grouping than outside it. Despite the likely pockets of density, it does not seem as though there would have been groupings for which interactions were *significantly* higher. Rather, they would have been only somewhat higher, with the densities fairly variable from generation to generation. Thus, if one deploys the causal interactionist population concept, Epling, Dobzhansky, and Wright were studying one continuous population rather than multiple populations (Figure 3.1).

Two considerations support this conclusion. The first is to suggest that while it is clear that many plants were not interacting directly, many would
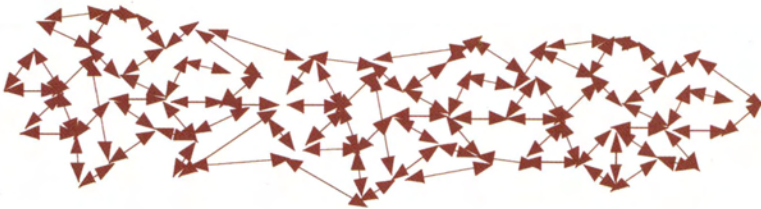
FIGURE 3.1 One Continuous Population Brown arrows represent survival and reproductive interactions. There are places where the interactions are "denser" but no places where the rates of interaction within a grouping are much higher than those outside a grouping.

have been interacting *indirectly*.[16] As an illustration of indirect interaction, suppose plant A takes resources that are no longer available to plant B, which might mean that plant B is not available to interbreed with plant C. Thus, plant A has interacted indirectly (or transitively) with plant C. Without any internal or external isolating mechanisms, such indirect interactions would suggest that the entire carpet was acting as a biological whole. Second, any pockets of density likely would be short-lived, which is not to say that they would not have effects or that the effects could not be ecologically or evolutionarily important.[17] But *sustained* ecological or evolutionary processes would not be expected within those groupings themselves.

Finally, I will make a brief note about evolutionary processes. The authors concluded that drift played a substantial role in the distribution of blue and white flowers. Recent studies, such as one by Schemske and Bierzychudek (2007), have challenged that conclusion. My suggestion is that claims about population structure should be distinct from claims about evolutionary process; that is, assuming the accuracy of Wright's results, in the 1940s in the Mojave Desert *L. parryae* formed a continuous population regardless of whether the distribution of blue and white flowers was due primarily to drift or primarily to selection. (Whether it forms continuous populations in other places and times would be an empirical question.) Indeed, in most of the case studies that follow, biologists made claims concerning the relative importance of selection and drift, but those claims are independent of claims concerning population structure. More precisely, a given population structure does not dictate whether selection and/or drift is operating, though it does dictate the organisms over which these evolutionary processes range.

Case 2: Populations with Only Survival Interactions

One of the reasons to have a population concept that includes survival interactions without requiring reproductive interactions is to enable it to account for the possibility that asexual reproducers form multiple populations. Of course, it may be that some (perhaps even many) asexual reproducers do not form separate populations and instead consist of only one population. The common wisdom for bacteria has been that microorganisms are ubiquitous and the global richness of microbial species is moderate (Finlay and Clarke 1999). However, this view has been challenged recently, suggesting that some bacteria do consist of multiple populations.

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[16] Note that "interacting indirectly" and factors that serve as "indirect indicators" for other factors are not the same thing, although in this case, there are indirect indicators (the distribution of plants in time and in space, plus what is known about the life cycle of *L. parryae*) that the plants would have been interacting indirectly.

[17] Indeed, these groupings might be groups that could engage in group selection; Shavit (2005) discusses the group concept.

One such challenge comes from a recent study of several *Pseudomonas* (*sensu stricto*) species (Cho and Tiedje 2000). *Pseudomonas* are free-living soil bacteria. Cho and Tiedje examined 85 different *Pseudomonas* genotypes from 38 transect samples of "undisturbed pristine soil" from 10 sites on 4 continents. Their results show that for each of the 85 genotypes, a particular genotype found in one 200-meter transect of a particular site would not be found at the other study sites or other continental regions. Moreover, the majority (91.8%) of genotypes were only found in one transect sample of a site and just 7 of the 85 genotypes were repeatedly isolated from different transect samples of the same site.

Cho and Tiedje state, "This indicates some mixing and dispersal of the genotypes within a site but not between sites and regions" (Cho and Tiedje 2000: 5455). If this statement is correct, their results suggest a remarkable amount of geographic isolation among groupings of particular *Pseudomonas* genotypes.[18] Although there are no reproductive interactions within these groupings, it is reasonable to assume there are survival interactions, such as competition for the same resources. If this is correct, then they form separate populations by the criteria of the causal interactionist population concept (Figure 3.2). Note that there are no direct observations of the sur-

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[18] Again, as with all of the cases described, I take no stand on whether the conclusions drawn are accurate; my claims for population structure would be different if the conclusions were different. For this case in particular, Douglas Futuyma (personal communication) suggests that an alternative reason for single-site distributions could be that mutations happen so fast that a genotype gets mutated out of existence soon after it has dispersed to a new location.
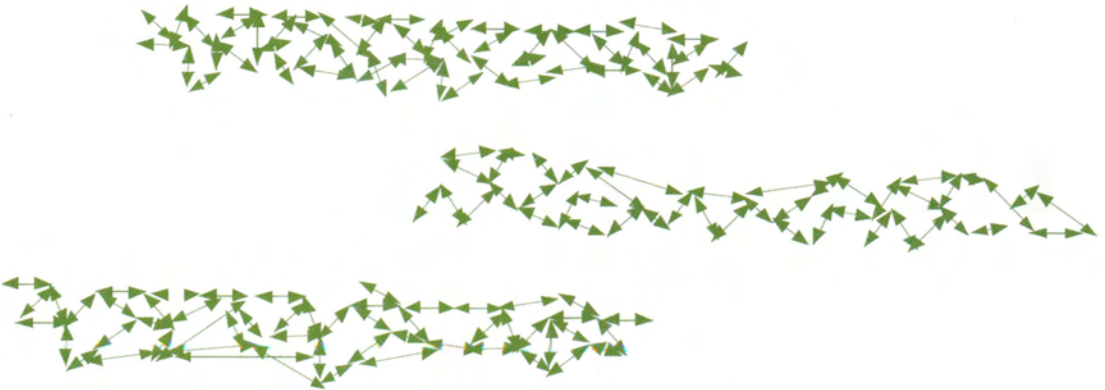
FIGURE 3.2 Multiple Populations Green arrows represent survival interactions; there are no reproductive interactions since the bacteria reproduce asexually. Groupings are geographically isolated from one another.

vival interactions, but that the genotype distributions, together with what is known about bacteria, form indirect evidence for the cohesiveness of the groupings.

Case 3: A Simple Metapopulation

Lamotte's 1950s investigation of *Cepaea nemoralis*, an often studied and widely distributed land snail, illustrates the causal interactionist metapopulation concept. In the Aquitaine region in southwestern France, Lamotte found groupings (what he called "colonies") that were 1 to 2 kilometers apart and well isolated chiefly through the requirement of shade, especially in the summer. The numbers of individuals in a grouping ranged from one to several hundred, with some larger. There was some migration between colonies, but in most cases, there was only a very limited amount:

> In the gaps between the colonies practically no Cepaea are found, or else
> only a few individuals or little groups of them, here and there, along
> the hedges running along the field boundaries, or upon shaded banks.
> The isolated individuals constitute what one may call 'migration trails'
> between populations and their very scattering shows the low frequency
> and discontinuity of these exchanges (Lamotte 1959: 66).

Lamotte describes a paradigmatic example of a metapopulation. The smaller groupings are local populations, with the rates of interaction (presumably both survival and reproductive) within the groupings being very much greater than among the groupings. There are also interactions among the local populations—the infrequent migrations from one to another—and their very infrequency relative to the frequency of interactions within the groupings implies that this is one metapopulation rather than one patchy population. However, the fact that there are *some* interactions among the local populations means that there is some cohesiveness to the whole; that is, if there were no such interactions, there would be no metapopulation, but instead only separate local populations (Figure 3.3).

In the three case studies examined so far, locations of organisms in space have played crucial roles as indirect indicators of causal interactions among organisms, which might lead one to conclude that geographical location ought to be part of the population and metapopulation concepts. However, as will be seen in the subsequent case studies, even though consideration of spatial location is always important, it is not always definitive.

Case 4: A Patchy Population

If the rates of interactions between groupings of organisms are lower, but not *significantly* lower, than the interactions within the groupings, the organisms do not form a metapopulation. Rather, they form one patchy population. A species that is organized into multiple patchy populations is the montane willow leaf beetle, *Chrysomela aeneicollis*, studied in the Sierra Nevada by Rank (1992) and later by Dahlhoff and Rank (2000) and
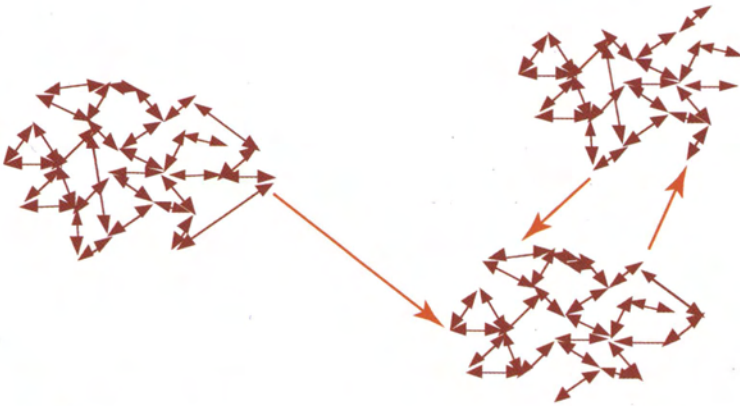
FIGURE 3.3 Multiple Local Populations Forming One Metapopulation The brown arrows that are within the groupings (i.e., the local populations) represent both survival and reproductive interactions, whereas the longer orange arrows between groupings represent migrations from one grouping to another. What makes this a metapopulation is that the latter exist but are much less frequent than the former.

Rank and Dahlhoff (2002). *C. aeneicollis* requires a moist habitat; the beetles can fly but do so only rarely. In the Sierra Nevada, *C. aeneicollis* can be found on willow shrubs; the shrubs are located in numerous physically separated bogs. The bogs themselves are located in one of three drainages, separated by high-elevation ridges that present a challenging (though not insurmountable) barrier for the beetles. Thus, there are groupings (on the shrubs) within groupings (in the bogs) within groupings (in the drainages). Genetic evidence (expressed using a modification of Wright's F_{ST}; see Footnote 12) shows that the differentiation at the drainage level is very much greater than at the bog level, which in turn is greater (but not significantly greater) than that at the shrub level.

With the genetic evidence serving as an indirect indicator of reproductive interactions and with survival interactions being a reasonable inference, these results suggest that each drainage contains a patchy population, with patches at the bog and shrub levels.[19] That is, it appears as though the rates of interaction *within the bushes* are greater (but not very much greater) than the rates of interaction *among the bushes,* and that the interactions *within the bogs* are greater (but not very much greater) than the interactions *among the bogs* (Figure 3.4).

Note that spatial location alone could not have dictated this result. If, for example, it were discovered that, contrary to Rank's (1992) findings, there

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[19] Also, given the evidence for minimal migration among the drainages, the three patchy populations in the drainages collectively form a metapopulation.
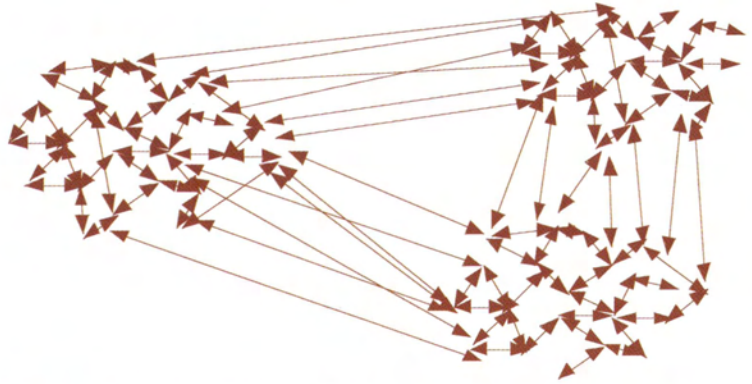
FIGURE 3.4 **A Patchy Population** The brown arrows represent survival and reproductive interactions as well as regular movements among groupings (which would be followed by further survival and reproductive interactions). The rates of interactions within the three patches shown are only somewhat greater than the rates of interaction among the patches. There is some further patchiness within each of the three patches, but again, it is not significantly greater than the interactions among them.

were significant genetic differentiation among the bogs, which would imply that the rates of interaction within the bogs were much higher than those among the bogs, then that would be evidence that populations formed at the bog level rather than at the drainage level. In other words, in principle, there could be the same distribution of organisms in space, but with different patterns of interaction and thus different entities operating as biological wholes.

Case 5: A Metapopulation of Reproductive Populations

I use the term *metapopulation of reproductive populations* to refer to cases in which organisms mate locally, but struggle (in a Darwinian sense) globally. The study by Kaliszewska et al. (2005) of the Southern Ocean right whale, *Eubalaena australis*, seems to be one such case. *E. australis* has three wintering locations for breeding (i.e., the coastal waters of Argentina, South Africa, and Australia), but in the summer, there are common feeding grounds in the Antarctic. The genetic evidence suggests that whales return to the same breeding grounds with some, but very little, migration among breeding groupings—one or fewer females per decade (Kaliszewska et al. 2005).

This case forms a bit of a puzzle. If one considers survival interactions alone, as occurs in the population concept defended by Gildenhuys (2009), there appears to be only one population because the whales are surely competing intensely at their feeding grounds. However, if one looks at reproductive interactions alone, there appears to be three populations, because there is very little reproductive interaction among the three breeding
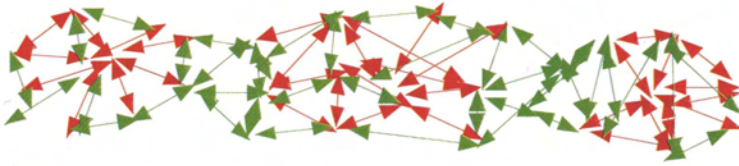
FIGURE 3.5 Multiple Reproductive Populations Forming One Metapopulation The red arrows are reproductive interactions; the green arrows are survival interactions. The organisms engaging in reproductive interactions are also engaging in survival interactions, but there are only survival interactions between these groupings. Thus, the rates of interaction of the former are much greater than those of the latter.

groupings. But considering the two types of interactions together resolves the puzzle, as there are *both* survival and reproductive interactions *within* breeding groupings but *only* survival interactions *between* breeding groupings. Thus, the causal interactions within the three breeding groupings are clearly significantly greater than those among the breeding groupings. In other words, the breeding groupings exhibit more cohesion, operating as a biological whole to a far greater extent than the feeding grouping. It follows that the breeding groupings represent populations (what I call reproductive populations), but the feeding grouping is also a biological whole—it is a metapopulation of reproductive local populations (Figure 3.5).

Note again that while geographical location is relevant, it is not entirely definitive. The whales range over much of the earth's oceans, but what is more significant for future evolutionary outcomes (i.e., for shared fate) is the fact that there are three groupings that hardly ever breed with one another.

Case 6: A Metapopulation of Survival Populations

A *metapopulation of survival populations* is the reverse of a metapopulation of reproductive populations; rather than mate locally and struggle globally, they struggle locally and mate globally. *Gasterosteus aculeatus*, the threespine stickleback fish that inhabits an Alaskan drainage, is an example of this type of metapopulation (Aguirre 2007, 2009). Aguirre found that phenotypes are associated with habitat type (consistent with known adaptations) but not with geographic distances. In contrast, quasi-neutral (microsatellite) genetic differences were associated with geographic distances but not with habitat type.

These results suggest that with respect to reproductive interactions alone, there is one continuous population with isolation by distance, which is similar to the previously discussed case of *Linanthus parryae*. However, with respect to survival interactions, organisms are struggling (again, in a Darwinian sense) most intensely within particular habitats; there are
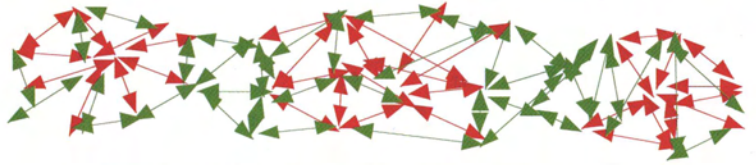
FIGURE 3.6 Multiple Survival Populations Forming One Metapopulation The green arrows are survival interactions; the red arrows are reproductive interactions. The organisms engaging in survival interactions are also engaging in reproductive interactions, but there are only reproductive interactions between these groupings. Thus, the rates of interaction of the former are much greater than those of the latter.

both survival and reproductive interactions within habitat groupings, but primarily reproductive interactions between habitat groupings. Thus, the causal interactions within the habitat groupings are clearly significantly greater than those among the habitat groupings. In other words, the habitat groupings exhibit more cohesion, operating as a biological whole to a far greater extent than the reproductive grouping. It follows that the habitat groupings represent populations (what I call survival populations), but the reproductive grouping is also a biological whole—it is a metapopulation of survival local populations (Figure 3.6).

Some Responses to Possible Questions

As concerns about my proposed causal interaction population concept may have arisen by this point, this section addresses some issues that may be troubling. To begin, one might well ask whether or not there is a continuum between a metapopulation and a patchy population, and if there will be some cases for which it is difficult to determine if a given population structure manifests the former or the latter. The answer is yes, there is a continuum, and the boundaries of the population are the *largest* grouping for which rates of interaction are *much higher* within the grouping than outside. A numerical value could be put on the relative strengths of those interactions (future work might consider how best to do this) to specify where to draw the line, but it is hard to see how any particular value could be defended. Any chosen numerical value would be fairly arbitrary, with little difference between slightly higher and slightly lower values, which implies that in *some* cases (how many remains to be seen) there will be no principled answer as to whether or not there is a metapopulation or a patchy population (alternatively, there could be many cases that are fairly clear-cut). However, this view does *not* imply that populations are arbitrary or that their boundaries can be drawn *anywhere*. It just means that populations are blurry entities, with edges that are not always well defined.

One might also ask if there is a difference between describing a particular population structure as one patchy local population or as a metapopulation of local populations. I have two responses. First, if it were equally correct to call a particular population structure a patchy population or a metapopulation—if one of these characterizations were not a *better* representation of the real world—then some claims concerning evolutionary processes (e.g., selection, drift) could not be judged as superior to other claims. For example, if the Alaskan threespine sticklebacks formed a patchy population (and not a metapopulation as I argued previously), we would calculate the expected average change over the whole population and understand selection in terms of that one overall trend (whatever it would be). But if the sticklebacks formed a metapopulation, then there would be numerous selection processes, with selection differing by local population. The outcomes that would be expected from those two scenarios (e.g., 10, 50, or 100 generations from now) would likely be very different from one another. This shows that different selection processes are implied by different population structures; presumably, one is a better representation of the actual evolutionary phenomena. Indeed, the different population structures yield different predictions, and one set of predictions is likely to be more accurate. However, these judgments can be made only if the difference between a patchy population and a metapopulation is recognized.

Second, regarding the issue of whether it makes a difference if we describe a particular population structure as one patchy local population or as a metapopulation of local populations, there is reason to think that metapopulation models may be distinctive in certain respects, as has been discussed by various authors.[20] In particular, researchers have argued that metapopulation models: (1) describe the ideal conditions for evolution (Wright 1931, 1932), (2) facilitate demonstrations of drift in nature (Lamotte 1959; Millstein 2008), (3) imply simultaneous use of predators in order to control pests (Levins 1969), and (4) predict regional persistence of locally unstable species (Harrison 1991). Collapsing the distinction between metapopulations and patchy populations assumes *a priori* that patchy populations would have these same implications, which they may or may not. By retaining both concepts, the possibility that there are different consequences for patchy population models and metapopulation models is preserved.

Of course, one might acknowledge the need to distinguish between patchy populations and metapopulations without accepting the causal

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[20] Hanski and Simberloff (1997) suggest that there may be some cases for which the consequences are "about the same" (e.g., a low rate of long-distance migration as compared to a high rate of short-distance migration). I do not deny this possibility, but would caution that an approach that focuses solely on the consequences of the model regardless of whether or not the assumptions of the model are met could raise problems later—others may misunderstand the simplification or there may be other consequences that are *not* "about the same."

interactionist population and metapopulation concepts. Reasons to accept the concepts argued for in this paper include the following. Obviously, a central feature of these concepts is their focus on *interactions*. Interactions among organisms are more significant than geographical location. Both humans and right whales live widely across the planet (albeit in very different habitats!), but their patterns of interaction differ in evolutionarily important ways. (This chapter has not included a discussion of population structure among humans, a complicated and interesting topic; however, the characterization of relatively distinct breeding groups that have survival interactions among all members would not characterize the present human configuration). The presence of interactions among a grouping of organisms also means that the grouping is acting as an individual (i.e., a biological whole); organisms have a shared fate to a degree. The population concept picks out that individual, and the interactions pick out groupings that are likely to differentiate in the future. For example, barring changes in population structure, we would expect further differentiation among the right whale breeding groupings and the stickleback habitat groupings. In addition to its focus on interactions, another benefit of the causal interactionist population concept is that it does not require reproductive interactions among organisms, so that the concept works for asexual as well as sexual populations. Finally, it does not assume any particular evolutionary process (e.g., selection, drift). Once the population is picked out, then the processes that are acting can be determined. Indeed, by forcing identification of populations (and defense of those identifications) prior to determining their evolutionary and ecological processes, the concept prevents predetermining the outcome of investigations though a convenient choice of population structure.

Conclusion

I hope to have gone a fair way toward establishing the causal interactionist concepts of population and metapopulation, yet there is admittedly much more work that needs to be done. There are more types of cases to be considered, some of which may necessitate modification or elaboration of the concepts, as occurred with the right whale and three-spine stickleback case studies. Another issue that needs to be addressed is the role that time plays in our understanding of populations; it may be that consideration of very short periods of time (taking into account ephemeral interactions) or very long periods of time will require further amendments to the population concept. Finally, there are numerous related concepts, such as organism, group, species, community, and the more general concept of biological individuality, which would enhance the understanding of population concepts. Other philosophers and biologists have worked on these concepts and continue to work on them; progress has been made but more needs to be done.

The length and vehemence of the debate over species concepts in particular (which is understandable, given the complexities of the topic) makes me humble about the prospects for progress on population and metapopulation concepts. However, it is my impression that work in the philosophy of biology continues to improve and that there are many productive interactions between philosophers of biology and biologists (as well as historians of biology). Philosophers of evolutionary biology are more attuned to biological practice than ever before. For those who seek conceptual clarity, it can be a difficult line to walk between the practical demands of theoretical biology and the logical demands of philosophy of biology, and some stray more to one side than the other, striving to find the right balance and perhaps not always achieving it. The fact that researchers struggle with the balance between theoretical biology and philosophy of biology should not be a surprise; each field involves difficult, yet important issues, and thus the intersection does as well. However, if we are to continue to work in a Darwinian vein (always with modifications and enhancements), we must continue to try to resolve them.

Acknowledgments

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