Populations as Individuals

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Abstract
Biologists studying ecology and evolution use the term "population" in many different ways. Yet little philosophical analysis of the concept has been done, either by biologists or philosophers, in contrast to the voluminous literature on the concept of "species." This is in spite of the fact that "population" is arguably a far more central concept in ecological and evolutionary studies than "species" is. The fact that such a central concept has been employed in so many different ways is potentially problematic for the reason that inconsistent usages (especially when the usage has not been made explicit) might lead to false controversies in which disputants are simply talking past one another. However, the inconsistent usages are not the only, or even the most important reason to examine the concept. If any set of organisms is legitimately called a "population," selection and drift processes become purely arbitrary, too. Moreover, key ecological variables, such as abundance and distribution, depend on a nonarbitrary way of identifying populations. I sketch the beginnings of a population concept, drawing inspiration from the Ghiselin-Hull individuality thesis, and show why some alternative approaches are nonstarters.

Biologists studying ecology and evolution use the term "population" in many different ways. Sometimes a population is any grouping[1] of conspecifics under investigation, but most biologists try to delimit the grouping in some way: by space and/or time, or interbreeding. For example, Wells and Richmond (1995) identify definitions of "population" in the biological literature that range from a very permissive definition ("a group of individuals of a single species"), to a grouping delimited only by a particular research investigation ("a somewhat arbitrary grouping of individuals of a species that is circumscribed according to the criteria of some specific study"), to one that invokes a spatial restriction ("group of organisms of the same species living in a particular geographic region"), to one that invokes a spatial and a temporal restriction ("all the members of a species that occupy a particular area at the same time"), to one that restricts by spatial and temporal criteria as well as potential for interbreeding ("any group of organisms capable of interbreeding for the most part, and coexisting at the same time and in the same place").

Yet, little philosophical analysis of the concept has been done, either by biologists or philosophers, in contrast to the voluminous literature on the concept of "species" (but see, e.g., Wells and Richmond 1995, Gannett 2003, Gildenhuys 2009). This is in spite of the fact that "population" is arguably a far more central concept in ecological and evolutionary studies than "species" is; it is the core concept of models in population genetics, ecological genetics, population biology, ecology, and evolutionary ecology. Populations are the entities that evolve, prior to any evolution of species, and they are the entities within which we study abundance and distribution. The fact that such a central concept has been employed in so many different ways is potentially problematic for the simple reason that inconsistent usages (especially when the usage has not been made explicit) might lead to false controversies in which disputants are simply talking past one another. For example, Pfeifer et al. (2007: 30) point out that Munguira and Martin (1999) fail to specify whether the population size of the butterflies they are studying refers to "the (maximal) number observed on a certain day during the flight period or the total number of all individuals which have belonged to the population within the whole flight period."[2] When Švitra (2008) revisits Munguira and Martin's study and comes to different conclusions, is that because the former considers the whole flight period but the latter considers particular days? Because the concept of population in play is unclear, the source of the disagreement is unclear. So there is a reason to think that attempting to define the concept of population is a worthwhile endeavor.

However, the inconsistent usages are not the only, or even the most important reason to examine the concept. Suppose, for example, that we were to deploy the most permissive of the definitions identified above, where a population is taken to be "a group of individuals of a single species"—a definition that implies that any arbitrary set of conspecifics can be taken to be a population. The problem with this definition is that it also renders selection and drift—processes that occur within populations—arbitrary.[3] To see this, consider the example of *Cepaea nemoralis*, a well-studied land snail. *C. nemoralis* is highly polymorphic, and in most places where it is found, pink, brown, and yellow color morphs can be observed. If any set of *C. nemoralis* can be the population, then a population could consist only of the pink morphs. In this case, there would be no selection or drift, since variation is a necessary condition for both selection and drift. Or it could consist only of the pink and brown morphs, which (let's suppose) are equally fit in the given environment. In this case, selection would not operate, but drift would, since there are physical differences between the morphs but not fitness differences. Or the population could consist of all three morphs, where (again, let's suppose) the pink and brown morphs are equally fit, but the yellow morphs are fitter than both the pink and brown ones. In this case, selection would tend to favor the pink morphs over the brown and yellow morphs, but the brown and yellow morphs would undergo drift with respect to one another. Thus, delimiting the population in three different ways yields three different answers to the question of whether selection and/or drift is operating: in the first case, it's neither drift nor selection; in the second case, it's drift without selection; and in the third case, it's both selection and drift.[4,5]

In short, if *any* (gerrymandered or otherwise) set of organisms is legitimately called a "population," our ascriptions of selection and drift are purely arbitrary. Indeed, there simply would be no fact of the matter about whether selection was operating or not. I take it that this is an unacceptable conclusion for anyone who thinks that selection can explain, as Darwin sought to explain, "the mutual relations of all organic beings to each other and to their physical conditions of life" (Darwin [1859] 1964: 80).[6] Moreover, key ecological variables, such as abundance and distribution, depend on identifying the population, and evaluating the potential strength of selection and drift requires knowing the size of the population. So, we need to delimit groupings of organisms somehow—but how? Can we characterize populations in a nonarbitrary way?

In answering this question, it is important to distinguish between two things that we could mean by "arbitrary": (1) Any set of organisms can be a population, including "gerrymandered" sets; and (2) there are difficulties in determining the edges of a population or difficulties in determining the exact number of populations in certain cases. I am seeking to avoid the former, but in certain cases, I am unlikely to be able to avoid the latter, which is more accurately termed "blurry edges" rather than "arbitrariness." Blurriness may simply be the biological reality with which we are faced in some situations.

My discussion here will of necessity be brief and a bit preliminary; indeed, I hope only to sketch the general form that a defensible definition of population might take, with further refinements to come later. Also, it should be clear that I am limiting my discussion to analyzing the concept of population in ecological and evolutionary contexts—the concepts of population in, say sociology or biomedicine, are undoubtedly different. Finally, for the sake of simplicity, I will consider only populations of organisms, although of course we might want to think about populations of many types of biological entities (e.g., populations of cells). This assumes that we can distinguish organisms from populations, an issue worthy of exploration in its own right, but which I will not explore here. Instead, I address only the situations where the organisms in question are uncontroversially biological individuals.

Six Starting Assumptions

I will begin by sketching six lightly defended assumptions that will serve to provide a starting point for analyzing the concept of population in ecological and evolutionary studies. With the exception of the first assumption, which I will defend in a little more detail, I take these to be generally held beliefs about biological populations.

First, populations are good prima facie candidates for being individuals in the Ghiselin-Hull sense.[7] For those not familiar with the Ghiselin-Hull individuality thesis[8] (see, e.g., Ghiselin 1974, 1997; Hull 1976, 1978, 1980), this may sound oxymoronic; it might be thought that the defining characteristic of a population is that it is a grouping of individuals, so how can a population itself be an individual? However, this worry assumes that "organism" and "individual" are synonymous; as Ghiselin (1974) points out, "individual" is better understood as "a particular thing." Thus, individual organisms can be made up of individual cells, but they are no less individuals because of that. Therefore, populations could be individuals while still being composed of individual organisms. Furthermore, Ghiselin (1974) clarifies, the United States of America is an individual, yet it is not physically continuous; thus, the fact that populations are not physically continuous does not prevent them from being individuals either. And, individuals are neither classes nor sets. Rather:

Individuals are spatiotemporally localized entities that have reasonably sharp beginnings and endings in time. Some individuals do not change much during the course of their existence, others undergo considerable though limited change, and still others can change indefinitely until they eventually cease to exist. But regardless of the change that may occur, the entity must exist continuously through time and maintain its internal organization. How continuous the development, how sharp the beginnings and endings, and how well-integrated the entity must be are determined by the processes in which these individuals function. (Hull 1980: 313)

To this characterization, I would add that the parts of individuals have a *shared fate*.[9] Because of the causal interactions among the parts of an individual, it will usually be the case that what affects one part affects some of (if not all) the other parts. It also seems to be the case that individuals must consist of at least two parts; otherwise, it would not make sense to speak of causal interactions. One might try to say that a part can interact with itself, but this would strip the notion of interaction of its full meaning. Of course, biology recognizes unicellular organisms as well as multicellular organisms, and this might seem to be a counterexample to my claim here, but in fact, unicellular organisms are quite different from multicellular organisms in many respects. We might well have chosen a different name for these biological individuals whose parts are not cells, but rather intracellular entities.

Using this view of individuals, we can see that populations are at least candidate individuals. They are spatiotemporally localized entities. They come into existence (generally with the founding of a new population, as might occur with geographical separation) and go out of existence (certainly with the death of the last organism in the population, if not sooner). Clearly, they change over time; indeed, ecology and evolution seek to describe those changes over time. If I am right about the nature of interactions, they will consist of at least two organisms. But are they integrated, cohesive[10] entities, and if so, to what degree? Are they continuous through time (i.e., are they historical entities)? Below, I will address these questions in order to make the case that populations are individuals in the Ghiselin-Hull sense.

Second, the concept of population should be at least somewhat different from the concept of species, to allow for cases where a species is composed of multiple populations. Of course, there may be certain cases where the species is composed of only one population—*homo sapiens* may be one such case—but this should not be true by definition. In what follows, I will not presuppose any particular definition of species in an attempt to provide a characterization of population that is neutral with respect to species definition.

Third, it is possible for an organism to leave one population and join another population; in other words, the definition of population has to deal with migration. Indeed, from a population genetics standpoint, migration is a cause of evolutionary change within a population.

Fourth, the concept of population should also be distinct from the concept of "metapopulation." Metapopulations are themselves boundary objects, as difficult to characterize as populations, communities, or ecosystems. However, we might begin by thinking of a metapopulation as a population (in a more general sense than the one being explored here) of populations of organisms, with limited migration between the "subpopulations" (so again, understanding how migration fits into the characterization of population is essential).

Table 1. Summary of candidate causal interactions for the concept of population.

Type of Causal Interactions	Candidate Interaction	Analysis
Reproductive interactions	Minimum gene flow out of the grouping	Outcome rather than process; hard to define independently of selection
	Potentially interbreeding organisms	Too strong; risks-making population concept identical to species concept
	Actually interbreeding organisms	Doesn't include all reproductive activities
	Actually mating organisms	A promising candidate, though may need to specify time span
Survival interactions	Struggle for existence, construed broadly to include both competitive and cooperative interactions	A promising candidate that will allow the concept of population to apply to asexual reproducers and recent migrants

Fifth, populations of organisms consist of conspecifics. This assumption simply recognizes that there are other concepts in biology that include organisms of different species, such as "community." Just as the concept of population should be different from the concept of species, it should be different from the concept of community.

Sixth, in order for the definition of population to avoid the unpalatable conclusion that selection and drift are arbitrary, it should be independent of selection and drift. For example, a definition of population characterized in terms of the relative strengths of migration to selection will not serve the intended purpose (it will be circular).

Toward Populations as Individuals

There are three basic types of population definitions that map onto three different ways in which one might seek to delimit a population:

1. *Boundary definitions*: For example, populations could be delimited by spatial boundaries and/or temporal boundaries.
2. *Causal interaction definitions*: For example, populations could be delimited in terms of the interbreeding among a grouping of organisms.
3. *Historical definitions*: For example, populations could be delimited by genealogical trees.[11]

Combinations of these three types are also possible. However, on the assumption that populations are individuals, only those that incorporate causal interactions (type 2) provide for the cohesion necessary for individuality. Spatially disjoint groupings may be sufficiently integrated, with a shared fate, if there is a fair amount of migration between them—but then this suggests that spatial location isn't the central issue for delineating populations. Nonetheless, spatial locations may be useful indirect indicators of populations. Historical definitions, on the other hand, track the outcomes of causal interactions, but do not themselves constitute causal interactions.

However, as Hamilton et al. (2009) argue, to say that an entity is an individual is the beginning of the analysis, not the end; one must specify the causal relations by which the parts that comprise the entity cohere into biological wholes. Thus, if populations are indeed individuals, it should be possible to specify the relevant causal interactions. So, let us consider candidates for causal interaction definitions. These fall into two broad categories: reproductive interactions and survival interactions. Table 1 summarizes the candidate interactions that I discuss below.

Considering reproductive interactions first, one obvious candidate, given its prevalence in population genetics models, is to define a population as the grouping out of which there is a very small amount of gene flow. Despite its common usage, minimal gene flow defines populations in terms of mating *outcomes* rather than in terms of causal processes that would cohere a population. Thus, it is not a candidate given the assumptions at hand, though it may (like spatial boundaries) often serve as a useful indirect indicator of a population. More worrisome is the need to specify what constitutes a minimal amount of gene flow. Generally, one considers the amount of gene flow relative to the amount of selection; however, as explained above, we are in need of a concept of a population that can be specified independently of evolutionary processes, or we risk circularity. So, minimal gene flow is not the causal interaction that we seek.

The next natural candidates, then, are the causal interactions that give rise to gene flow. For example, we might consider populations to consist of whichever organisms that can potentially interbreed. However, considering that even Mayr's (1996: 264) Biological Species Concept—"species are groups of [potentially] interbreeding natural populations that are reproductively isolated from other such groups"[12]—acknowledges that "isolating mechanisms do not always prevent the occasional interbreeding of non-conspecific individuals," such a definition would be far too strong. Again, whatever populations are, we think that it is possible to have species that consist of more than one population, so our definition of

population needs to be different from (and certainly weaker than) our definition of species.

So, instead of "potential interbreeding organisms," we might consider "actual interbreeding organisms" as appropriate for characterizing populations. However, as Griesemer (2002) argues, reproduction is a process, and mating is a part of that reproductive process. Consider, for example, that engaging in an *unsuccessful* mating ritual still constitutes a causal interaction that can affect the reproductive futures of the organisms involved. Thus, actually breeding is too strong a criterion.

This suggests that populations might consist of organisms that are actually mating, including mating rituals both successful and unsuccessful.[13] However, an immediate problem arises. At any particular moment in time, there might not be very many organisms engaged in mating rituals, especially given the large number of species that only mate during certain seasons. So, while mating is a relevant causal interaction, if we only consider mating at particular points of time it will not provide sufficient cohesion for individuality, even on a very generous account of individuality. Moreover, it would not appear to be continuous; the population would come into and go out of existence depending on mating interactions. However, we might consider mating interactions over a span of time. But what is the appropriate time span? One promising suggestion is to define the time span in a species-appropriate way (e.g., length of mating season or length of a generation for that species).

Of course, as the species literature has long recognized, using reproductive interactions as the only type of criteria means limiting one's definition to sexually reproducing organisms. This suggests that we ought to consider survival interactions as well in order to account for asexually reproducing populations. Indeed, reflection on the suggestion that populations might be individuals dictates that we consider survival interactions, since any causal interactions can cohere parts into a whole such that they have a shared fate. And, as Darwin's concept of a "struggle for existence" ([1859] 1964) has highlighted, there are many important causal connections among conspecifics that are related to survival without being (directly) related to reproduction.[14] These contribute to the cohesiveness of the whole. For example, conspecifics may be competing for the same limited resources; one organism's attainment of a limited resource may prevent other organisms from obtaining that resource. Thus, this represents a causal interaction among the organisms in question, and it highlights the way in which the parts of a population (i.e., the organisms) have a shared fate in the sense described above. Or, we may construe "struggle for existence" broadly to include cooperative interactions where organisms "struggle together." So, if organisms are competing for limited resources or cooperating for joint survival, then it seems reasonable to consider them to be a part of the population even if they are not mating or do not share a very recent

common ancestry with other organisms that are a part of the population.[15]

The preceding considerations lead me to make the following proposal:

Populations (in ecological and evolutionary contexts) consist of at least two conspecific organisms who, over a species-appropriate time span, are mating or are engaged in a Darwinian struggle for existence, or both.[16] The population is the largest number of organisms who are causally interconnected. Organisms who are located in the same spatial area (including recent migrants) are part of the population if and only if they are engaged in causal interactions with other conspecifics.

A few comments about my proposed definition are in order. Michael Ghiselin (personal communication, 15 March 2008) has suggested to me that one selfing hermaphrodite might be a counterexample to this definition. For the reasons stated above, I am still inclined to think that it does not make sense to think of one organism as a population, but the example warrants further consideration. The phrase "species-appropriate time span" has deliberately been left vague as a placeholder for future analysis, but again, the length of a mating season or the length of a generation for the species in question seem like promising candidates. The requirement that the population be the largest number of organisms who are causally interconnected specifies a unique bounding of the population, with the caveat mentioned at the outset that many populations will have blurry edges. This requirement might fruitfully be spelled out in terms of Simon's (2002) concept of "nearly complete decomposability," which in this context would mean that population consists of the organisms whose rates of interaction are much higher among each other than they are among other organisms.[17] And, while continuity (one of the requirements for individuality) is not mentioned in the definition explicitly, it follows from the incorporation of causal interactions among organisms. Because the interactions aren't necessarily reproductive, however, the continuity isn't necessarily genealogical (as it is on some definitions of species).

Final Thoughts

Given the length and vehemence of the debate over species definitions, I harbor no illusions that this short article will have settled the question of what a population is. Instead, I offer it in the spirit of beginning the dialogue, not ending it. I have provided some reasons why I think that populations should be understood as individuals, and fleshed out what I take to be the relevant causal interactions (namely, mating interactions and "struggles for existence"), indicating places where I think future work is needed. Of course, one might think that populations aren't individuals at all, but if so, why not? They seem to fit all of the characteristics of individuals, so the burden of proof is on my future critics to show in what ways they do not

fit. Alternatively, I may not have characterized the right set of causal interactions. For example, Gildenhuys (2009) offers an analysis of populations similar to that of my own, but he limits the type of interactions to what he calls "competitive causal interactions." His position is well defended, but I see no reason to exclude mating interactions. Or, one might think that there are other relevant causal interactions that I have missed. If so, "the more the merrier" (i.e., the more cohesive population, and thus, the better the case is for individuality)—I would happily expand my account to incorporate such interactions. Or, one might argue, as Gannett (2003) has, that different biologically and theoretically informed research questions might yield different and equally cogent definitions of population. Although I lack the space to respond to Gannett's detailed and historically informed arguments here, my thought is that while this may turn out to be the case, I'd like to see if one definition can do the job. Otherwise, a huge burden will rest on characterizing what constitutes legitimate biologically and theoretically informed research. If any research goes, then surely there could be research questions in ecology and evolution, which could make use of a gerrymandered set of organisms, with the consequence (as I discussed above) that attributions of selection and drift are arbitrary. That is a consequence that I, and I think most other biologists and philosophers of biology, would want to avoid.

Notes

1. I use the term "grouping" here and below rather than "group" in order to leave space for future analyses of the term "group" with respect to group selection. Thanks to Peter Gildenhuys for the suggestion.

2. Pfeifer et al. (2007), thus, argue for a concept of population that has time and space as explicit parameters.

3. Some of the other definitions, in particular "a somewhat arbitrary grouping of individuals of a species that is circumscribed according to the criteria of some specific study" and "group of organisms of the same species living in a particular geographic region," arguably generate the same problem if "criteria of some specific study" and "a particular geographic region," respectively, are understood loosely.

4. Wells and Richmond (1995) characterize other problems that arise from arbitrary delineations of a population.

5. A possible example of different delineations of populations leading to different conclusions about selection and drift is Hofer et al.'s (2009) argument that large allele frequency differences between *human continents* occurred by drift, rather than being due to natural selection and adaptation to *local environments*, as previous studies had contended.

6. For an alternative view, see Walsh (2007).

7. Indeed, it might be the case that if selection and drift are population-level causal processes (as I have argued elsewhere; Millstein 2006), then populations must be individuals.

8. It should be noted that this thesis was originally developed to address the nature of species, but it has since been extended to deal with biological entities such as colonies (Hamilton et al. 2009) and ecosystems (Odenbaugh 2008).

9. Here the reader should avoid inferring any suggestion of predestination in the term "fate" (Wiley 1978 also invokes "shared fate" for the species concept).

10. Mishler and Brandon (1987: 400) 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. 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."

11. One might think that there is a fourth type: reproductive isolating mechanism definitions. However, these are too strong; these criteria are invoked for species definitions. Again, our definition of population should be different from our definition of species.

12. Note that whereas Mayr (1996) used the term "population" as part of his definition of "species," I think it makes more sense to use the term "species" in the definition of "population." Obviously, one would not want to do both.

13. It might also be appropriate to include offspring-rearing activities here; see, e.g., Roughgarden (2009).

14. In invoking "struggle for existence," it might appear as though I have violated my sixth assumption, viz., that selection should not be a part of the definition of population. However, I am only invoking one of the necessary conditions for selection, not all of them. See Lennox and Wilson (1994) for a useful explication of the phrase "struggle for existence" and for a defense of the claim that "struggle for existence" is required for natural selection.

15. I am less sure about what to say about common climatic factors, which are also part of Darwin's concept of a "struggle for existence." These involve a shared fate (including a "check" on the numbers of organisms), but not necessarily any causal interaction among organisms as a result. In such cases, there may be an entity acting as a collective (see Note 9) that warrants the name "population."

16. My account of populations has some similarities to Templeton's (1989) concept of cohesion species, though it is not identical to it and does not rely on it.

17. Thanks to Jim Griesemer for this suggestion. Clearly, this needs further fleshing out, especially regarding differentiating between metapopulations and single populations with areas of greater integration. Again, the distinction will not be a sharp one.

Acknowledgments

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