

Discussion

Jacob Stegenga—“Population” Is Not a Natural Kind of Kinds (*Biological Theory* 5: 154–160, 2010)

Should We Be Population Pluralists? A Reply to Stegenga

Robert L. Millstein

Department of Philosophy
University of California, Davis
Davis, CA, USA
RLMillstein@UCDavis.edu

In “‘Population’ is Not a Natural Kind of Kinds,” Jacob Stegenga argues against the claim that the concept of “population” is a natural kind and in favor of conceptual pluralism, ostensibly in response to two papers of mine (Millstein 2009, 2010). Pluralism is often an attractive position in the philosophy of science. It certainly is a live possibility for the concept of population in ecology and evolutionary biology, and I welcome the opportunity to discuss the topic further. However, I argue that the case for conceptual pluralism has not yet been made. In what follows, I first clarify the issues at stake before taking up the topic of conceptual pluralism and responding to Stegenga’s criticisms of the causal interactionist population concept.

Clarifications

Stegenga directs the bulk of his comments toward Millstein (2009); thus it is important to clarify what that paper did and did not say, as well as clarify the issues that are at stake. First, despite the title of Stegenga’s paper, nowhere did I claim that the concept of population is a natural kind.¹ As Hacking (2007) demonstrates, the term “natural kind” has had many meanings, to the point where Hacking argues the term ought to be abandoned. I do not know what concept of natural kinds Stegenga is using, but on one common view of natural kinds, they have essences and can be described in terms of necessary and sufficient conditions. I certainly did not state, and do not think, that populations have essences or that they can be de-

scribed in terms of necessary and sufficient conditions. Indeed, I made sure to point out, as a matter of biological reality, that there can be cases in which there are difficulties in determining the edges of populations or the number of populations, and I discuss such cases in further detail in Millstein (2010). The concept I defend, drawing on Simon (2002), describes the boundaries of a population in terms of the largest grouping for which the rates of survival or reproductive interactions are much higher within the grouping than outside. This is hardly the stuff of essences and necessary and sufficient conditions. If, despite this, I am somehow unintentionally implying that populations are natural kinds in some more attenuated sense, it needs to be shown what sense that is. In addition, the case needs to be made that an argument *for* conceptual pluralism about populations is equivalent to an argument *against* the concept of “population” being a natural kind in this yet-to-be-determined attenuated sense, as Stegenga seems to assume. For my part, I claim only that populations are individuals, in the Ghiselin–Hull sense of the term (see, e.g., Ghiselin 1974, 1997; Hull 1976, 1978, 1980), and that they are the real entities that act (more or less) as a unit, i.e., they are biological wholes.

Second, Stegenga maintains that I motivate my positive account of populations by arguing against conceptual pluralism with respect to populations. This is true only if one equates “conceptual pluralism” with “anything goes,” which I do argue against; as I discuss further below, “anything goes” is a form of conceptual pluralism, but arguably not the most defensible form. Moreover, the *main* point of the Millstein (2009) essay was to argue that populations are individuals,² using all the criteria for individuality (taken together, not one at a time as Stegenga seems to imply) and to show how a concept of population could be developed out of it. I acknowledged that the concept had yet to be defended; the more extensive defense comes in the much longer paper (Millstein 2010), where I show how the concept of population (and metapopulation) that I defend illuminates six very different biological cases and further defend the need for the concepts of population and metapopulation. Stegenga cites the later paper but does not really address the arguments in it.

On Conceptual Pluralism

As noted above, Stegenga seems to equate “conceptual pluralism” with “anything goes” views. I do think, as I say in Millstein (2009), that there is a serious problem with the claim that any set of organisms (including “gerrymandered” sets) can *legitimately* be considered a population. And as I demonstrate there, if it were true that if any collection of organisms whatever could *legitimately* be considered as a population, then there would be no fact of the matter about whether selection was operating or not,³ and that this would raise a problem for anyone who thinks that selection can explain adaptation (or that it can explain anything at all). Stegenga seems to agree that there would be a problem with any claim that implies that there is no fact of the matter about whether selection is operating or not (or, at least, he thinks that it would be “odd” if there were no fact of the matter about whether selection is operating or not). However, he changes the antecedent “if any set of organisms is *legitimately* to be called a population” to “if we permit conceptual pluralism with respect to population,” thus equating “conceptual pluralism” with an anti-realist “anything goes.” And, so while he is right that “our *choice* of definitions does not influence aspects of the world independent of our knowledge of them” (emphasis added), it is still the case that if it were possible to *legitimately* call any set whatever a population, then selection would be arbitrary. It would not be our *choice* that made selection arbitrary, but rather that there was no fact of the matter about what the population was (allowing for any legitimate ascription whatever), so that there would be (1) no selection or drift on a “population” of pink morphs, (2) no selection but drift in the “population” of pink and brown morphs, and (3) both selection and drift in the “population” of pink, yellow, and brown morphs, where yellow morphs are the fittest, pink and brown morphs are equally fit, and the pink, brown, and yellow morphs referred to in each of the three purported “populations” are the same organisms.⁴ Unless Stegenga wants to accept the “odd” consequence that there are cases where there is no fact of the matter about whether selection is operating, I can’t see how he can avoid rejecting the “anything goes” form of conceptual pluralism.

There are, however, far more interesting forms of conceptual pluralism, such as the one defended by Gannett (2003), in which different biologically and theoretically informed research questions might yield different and equally cogent definitions of population.⁵ In Millstein (2009), I acknowledge that nothing that I say overturns this form of pluralism. Rather, I raise one brief worry for it, namely that if we do not put some limitations on what counts as “biologically and theoretically informed research questions,” then “conceptual pluralism” will slide into “anything goes.”⁶ I do not think Gannett endorses an “anything goes” view of populations. It may indeed be possible to specify what counts as biologically and theoretically in-

formed research so that an “anything goes” form of conceptual pluralism can be avoided; contra Stegenga, I don’t think this requires solving Popper’s demarcation problem. I just think it’s a difficult issue that has yet to be addressed, and I hope that Gannett (and/or others) work toward addressing it in this context.

Other than this brief reply to Gannett, the only way in which my papers argue against conceptual pluralism is indirectly, by making the positive case for a concept of population. Again, this is largely done in Millstein (2010), and yes, I still think that there is more to be said. As I think both papers make clear, I sought to jump-start a desperately needed conversation about the concept of population. It may ultimately turn out that one concept (or my proposed concept) cannot do the job. But then one needs to make the case for other, *defensible* concepts of population; conceptual pluralism taken as the obviously correct position or “anything goes” pluralism won’t do. One also can’t defend conceptual pluralism simply by pointing out that biologists disagree about the concept of population (as it sometimes seems that Stegenga is doing); this is, in fact, the starting point of my own analysis. It should not need to be stated, but all uses are not necessarily *good* uses, and clearly our language needs some limits, or we could just use cells, organisms, populations, species, etc., interchangeably—this is a conceptual “anything goes” *reductio*. I consider it a philosophers’ job (understood broadly to include conceptually inclined biologists) to differentiate the good uses from the bad ones. Stegenga calls this “linguistic policing”; I prefer to think of it as linguistic clarification, something of value to philosophers and biologists alike. Moreover, while I heartily believe that we ought to respect the terminological uses of biologists as well as their biological practices, in this case we simply cannot respect all such practices, especially since some biologists *themselves* are concerned about the proliferation of uses (e.g., Wells and Richmond 1995; Pfeifer et al. 2007), and since most biologists would not find acceptable the consequence that there is no fact of the matter about whether selection occurs.

Finally, Stegenga is surely right to point out that I endorse a type of pluralism by limiting the concept I defend to evolutionary and ecological contexts. Since I am not an “anti-pluralist,” I have no problem with that. My claim is only that ecological and evolutionary processes themselves have formed biological objects (in this case, populations) that operate more or less as a unit, and that our concept should reflect those objects as best as they can. Perhaps a broader concept of population is available to cross disciplines, and perhaps it would serve the purposes of scientific communication to use such a concept; I have no objection to such a concept. I simply think that a concept of population that could apply to, e.g., statistics, biomedicine, and ecology/evolutionary biology, would be so general that it would no longer serve the purpose of helping us

understand the models of ecology and evolutionary biology, nor would it tell us much about the entities that we were picking out to study, or give us guidance in making those choices in the first place.

But perhaps Stegenga has given reasons to think that my proposed population concept, which I have dubbed the *causal interactionist population concept* (Millstein 2010), is inadequate, which might be seen as providing some degree of support for some version of conceptual pluralism. Thus, let us turn to Stegenga's objections.

Replies to Concerns with the Causal Interactionist Population Concept

Stegenga raises three objections to the causal interactionist population concept. The first objection is that it is vague. I must admit that I find myself baffled by Stegenga's arguments in this section, and here I can only point out to the reader what may be obvious; Stegenga has taken bits and pieces of my concept and argued for their vagueness, rather than considered the whole. So, for example, he states that “[t]he notions of ‘Darwinian struggle for existence,’ ‘causally interconnected,’ and ‘same spatial area’ are loose enough to allow nearly any two conspecific organisms to be part of the same population.” But this follows only if one ignores the part that says, “The population is the largest number of organisms who are causally interconnected” (Millstein 2009: 271); as I hint at in the Millstein (2009) paper and state more firmly in the Millstein (2010) paper, the “boundaries of the population are the largest grouping for which the rates of interaction are much higher within the grouping than outside” (p. 67). Similarly, he first states that “causally interacting” is vague, before acknowledging that I did, in fact, specify the relevant types of causal interactions (survival and reproductive interactions—so, no, gravitational forces don't count), which he then admits are *not* conceptually vague. More usefully, Stegenga suggests that my concept is epistemically vague, pointing out that biologists often lack epistemic access to the relevant interactions. It is true that they often lack such access, an issue that I address in the Millstein (2010) paper by discussing the role that *indirect indicators* of these interactions can play without their being part of the concept of population. This sort of point is well recognized in the species literature; for example, in applying the biological species concept one might in certain cases need to rely on morphological characteristics.

The second objection that Stegenga raises is that the causal interactionist population concept does not in fact address some of the concerns that motivated me to propose the concept in the first place. For example, Stegenga suggests that individual organisms may sometimes display the relevant causal interactions necessary to be considered part of the same population, whereas at other times they may not, and that this may

set up situations where biologists could reach contradictory conclusions concerning the very same organisms—and I had expressed a concern about biologists talking past one another by inadvertently using different population concepts. Here I acknowledge that

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 (Millstein 2010: 82).

But to speak to Stegenga's concern, let's suppose that at time t_1 organisms are interacting in such a way that they would be considered a population on my account, but that at time t_2 their *descendants* (note that on my account, interactions need only occur over the course of a generation, not at any given moment in time) are no longer interacting in this way. Perhaps subgroups are interacting (in which case, we might say that the population has split), or perhaps all of the organisms have gone their separate ways, so to speak. Then a biologist who had studied the organisms at time t_1 might have identified certain selection processes, whereas another biologist who had studied those organisms' descendants at time t_2 might conclude that those selection processes were not operating. I don't see why this is problematic or contradictory. In fact, it seems exactly what we would want to occur. Indeed, it is a population concept that *reveals* the issue in the first place; otherwise, we might simply conclude that any descendants are members of the same original population and think that they are likely to be undergoing the same ecological and evolutionary processes (not that I think biologists would make such a mistake, given the relevant information). And acknowledging that population structure changes over time does not imply that there is no fact of the matter about which ecological and evolutionary processes are occurring at a specified time.

The third objection that Stegenga raises is that the causal interactionist population concept is overly restrictive “for the broad array of population-based questions that many ecologists (and geneticists, and epidemiologists, etc.) are interested in.” Again, the scope of the concept that I defend extends only as far as ecological and evolutionary contexts; I make no claim for population concepts outside that domain (indeed, I suspect that they are in fact different). But perhaps there are ecological and evolutionary questions that my concept does not address. If so, Stegenga has not identified them. He suggests that an ecologist might have reasons to study brown *Cepaea nemoralis* morphs alone, even if they are engaging in frequent survival and reproductive interactions with pink and yellow morphs: “Maybe they have special resistance to predation? Maybe they are less heat tolerant?” I agree that a biologist might be interested in these questions. However, the way they are phrased, they are asking about *relative* resistance to predation,

and *relative* heat tolerance; I can only imagine that the biologist is interested in these abilities relative to other organisms that the brown morphs are interacting with. If that is not so, or if the biologist is interested in those abilities in some sort of absolute (rather than relative) sense, then the biologist is no longer asking ecological or evolutionary questions. The biologist is asking questions that might better be described as behavioral or physiological ones. These kinds of questions have *implications* for evolution and ecology, of course, but only when other organisms that are engaged in frequent interactions are considered. As for studying subsets of what I call populations in order to determine their evolutionary processes (another one of Stegenga's suggestions), as I argue in the Millstein (2010) article, the "answers" that one arrives at will be highly misleading and will tend to be predictively inaccurate, because causal interactions relevant to evolutionary outcomes are not taken into account. Finally, I acknowledge that some biologists do refer to multi-species groupings as populations; my contention is only that there is already a perfectly respectable term in ecology and evolutionary biology to refer to such groups: community. Again, by reserving a different term for multi-species and single-species groupings, we leave conceptual space for the different dynamics that the former may have as compared to the latter. For example, even though predators and prey interact in ways that affect each other's survival, in general we don't expect such communities to have the same dynamics that populations of the same species do. For the communities that do have similar dynamics to those of populations, we will want to characterize the special circumstances that produce the similar dynamics. But to automatically assume the dynamics are the same (which is what we'd be doing if we failed to distinguish between communities and populations⁷) would result in pretty bad predictions in many cases.

Conclusion

The concept of population is absolutely central to the disciplines that study ecology and evolutionary biology, such as population genetics, ecological genetics, population biology, and evolutionary ecology. It is the concept that many of the models used in these areas are *about*. The models seek to track the dynamics of these populations and make predictions about their futures. Furthermore, populations are the entities that these biologists study in the field; when they sample, it matters whether they are samples of the same population or different ones. There may be more general concepts, applicable beyond ecology and evolutionary biology, that might be interesting for certain purposes, but they would not be informative for understanding what it is that ecologists and evolutionary biologists are tracking. And there might be more specific concepts, but these risk ignoring causal interactions that are relevant to the

outcomes under study. If there are other considerations that lead us to reject the causal interactionist population concept, or to accept it as one among other defensible concepts, the case has not yet been made.

Notes

1. Also, since I explicitly argued that populations are individuals, clearly I do not think that particular populations are kinds.
2. Thus the title, "Populations As Individuals"—I am baffled by Stegenga's statement that he's "not sure what hangs on this [claim] for Millstein" when it was the main point of the essay.
3. This is what Stegenga refers to as FOTM (1); FOTM (2) is an incorrect reading.
4. The example is inspired by the studies of *Cepaea nemoralis* in the 1950s; see Millstein (2008) for analyses of these studies. And just in case it wasn't clear, those are scare quotes around the term *population*.
5. The distinction between "anything goes" conceptual pluralism and more sophisticated forms in which certain concepts are defensible, and others are not, is one that is well recognized in the species literature. (See, e.g., Kitcher 1984; Mishler and Brandon 1987; Ereshefsky 1992). Even Dupré's (1981) "promiscuous realism," which is about as liberal a conceptual pluralism as I think you will find in the species literature, is not an "anything goes" conceptual pluralism (although it does go beyond the present concerns for a concept relevant to biological practice).
6. Stegenga seems baffled as to why I claim that, if we permit conceptual pluralism with respect to population, it follows that a huge burden will rest on characterizing what constitutes legitimate biologically and theoretically informed research. The answer is simply that I was replying to Gannett's (2003) account, which is clear from the context of my remarks.
7. Of course, we could distinguish between "single-species populations" and "multi-species populations"; my point is only that we should make the distinction. Not much hangs on the names themselves, aside from clarity and consistency with much (admittedly, not all) contemporary usage.

References

- Dupré J (1981) Natural kinds and biological taxa. *Philosophical Review* 90: 66–90.
- Ereshefsky M (1992) Eliminative pluralism. *Philosophy of Science* 59: 671–690.
- Gannett L (2003) Making populations: Bounding genes in space and in time. *Philosophy of Science* 70: 989–1001.
- Ghiselin MT (1974) A radical solution to the species problem. *Systematic Zoology* 23: 536–544.
- Ghiselin MT (1997) Metaphysics and the Origin of Species. Albany, NY: SUNY Press.
- Hacking I (2007) Natural kinds: Rosy dawn, scholastic twilight. *Royal Institute of Philosophy Supplement* 61: 203–239.
- Hull DL (1976) Are species really individuals? *Systematic Zoology* 25: 174–191.
- Hull DL (1978) A matter of individuality. *Philosophy of Science* 45: 335–360.
- Hull DL (1980) Individuality and selection. *Annual Review of Ecology and Systematics* 11: 311–332.
- Kitcher P (1984) Species. *Philosophy of Science* 51: 308–333.
- Millstein RL (2008) Distinguishing drift and selection empirically: "The great snail debate" of the 1950s. *Journal of the History of Biology* 41: 339–367.

- Millstein RL (2009) Populations as individuals. *Biological Theory* 4: 267–273.
- Millstein RL (2010) The concepts of population and metapopulation in evolutionary biology and ecology. In: *Evolution Since Darwin: The First 150 Years* (Bell MA, Futuyma DJ, Eanes WF, Levinton JS, eds), 61–86. Sunderland, MA: Sinauer.
- Mishler BD, Brandon RN (1987) Individuality, pluralism, and the phylogenetic species concept. *Biology and Philosophy* 2: 397–414.
- Pfeifer MA, Henle K, Settele J (2007) Populations with explicit borders in space and time: Concept, terminology, and estimation of characteristic parameters. *Acta Biotheoretica* 55: 305–316.
- Simon HA (2002) Near decomposability and the speed of evolution. *Industrial and Corporate Change* 11: 587–599.
- Wells JV, Richmond ME (1995) Populations, metapopulations, and species populations: What are they and who should care? *Wildlife Society Bulletin* 23: 458–462.

Lindsay Craig—The So-Called Extended Synthesis and Population Genetics (*Biological Theory* 5: 117–123, 2010)

Extended Synthesis: Theory Expansion or Alternative?

Gerd B. Müller

Department of Theoretical Biology
University of Vienna
Vienna, Austria
gerhard.mueller@univie.ac.at

Massimo Pigliucci

Philosophy Program
City University of New York
New York, NY, USA
massimo@platofootnote.org

In her critical essay on the Extended Synthesis in evolutionary theory, Craig (2010) argues that the concepts currently highlighted by EvoDevo represent significant and even insurmountable challenges to population genetics and, hence, to the core theoretical basis of the Modern Synthesis. Therefore she concludes that the ongoing conceptual developments in evolutionary biology are not appropriately described as an extension to the Modern Synthesis framework but represent a more substantial form of theory change.

Craig's position falls squarely into one of the three kinds of reactions we received concerning our edited volume (Pigliucci and Müller 2010) and the usage of the term Extended Synthesis. A frequent reaction is agreement with our main argument that evolutionary theory has significantly changed under the influence of new concepts emerging from multiple fields of evolutionary study, accepting our contention that population

genetics has a valid part in the newly emerging framework, but that the additional models and concepts expand both the formal structure and the explanatory content of the Modern Synthesis. Disagreement with our position comes in two categories. One is the (more frequent) view that the conventional theory already covers all significant parameters of evolution and, therefore, nothing substantially new can have happened in evolutionary theory. Representatives of this view fervently argue that no change in the traditional framework is required and, hence, any talk of "extension" is superfluous (e.g., Hall 2000; Coyne in Pennisi 2008 and in Whitfield 2008; Minelli 2010). The second group of dissenters, including e.g., William Provine, a highly respected historian of the Modern Synthesis who felt strongly that our project was not radical enough (personal communication, December 2008), argue the opposite: the present challenges to the received theory are so substantial that no reconciliation with the classical framework is at all possible. Advocates of this view find themselves forced to contend that the Modern Synthesis needs to be supplanted by a new theory, and some propose in line with Craig that EvoDevo provides the kind of theory that could achieve this. We wish to make a brief comment on each of these two views.

The nothing-substantially-new position is the more surprising one. It effectively argues that seven decades of advancement in biological research have left no trace on a theory coined in the 1930s and 1940s. Even some firm supporters of EvoDevo deny that its conceptual consequences could in any way represent a challenge to the Modern Synthesis paradigm (Hall 2000; Minelli 2010). In an unlikely association, they are assisted by the die-hard population geneticists like Jerry Coyne and Michael Lynch (e.g., Lynch 2007; see Pigliucci 2008), who either dismiss new ideas about evolvability, robustness, modularity, and the like or—without a trace of detecting the inherent self-contradiction—dismiss those same ideas as straightforward derivations from the Modern Synthesis. Clearly, both criticisms cannot be on target simultaneously, and the skeptics here have the onus of seriously engaging the now substantial literature on evolvability and related concepts if they wish to deny its validity. Science does not make progress via armchair dismissal.

The more-change-is-needed position defended by Craig and others has a number of points in its favor. In fact, several of our colleagues would agree that some of the new concepts included in the Extended Synthesis contain aspects that go beyond a strictly Modern Synthesis explanation. Think of epigenetic inheritance, non-gradualistic modes of change, multilevel selection, or non-adaptive forms of character generation. However, does the inclusion of factors that permit different forms of organismal change justify a complete rejection of the earlier model? Craig's argument is strongly focused on EvoDevo. She more or less equates the conceptual changes afforded by