How the Concept of 'Population' Resolves Concepts of 'Environment'

Roberta L. Millstein
Department of Philosophy
University of California, Davis
Davis, CA 95616
RLMillstein@UCDavis.edu

Abstract: Millstein (2009, 2010) defends the "causal interactionist population concept" (CIPC). Here I further defend the CIPC by showing how it clarifies another concept that biologists grapple with, namely, *environment*. Should we understand selection as ranging only over homogeneous environments or, alternatively, as ranging over any habitat area we choose to study? I argue instead that the boundaries of the population dictate the range of the environment, whether homogeneous or heterogeneous, over which selection operates. Thus, understanding the concept of "population" helps us to understand concepts of "selective environment," exemplifying the importance of the CIPC to other concepts and debates.

1. Introduction

Philosophers of science have been exploring the concept of "species" for decades, but the related and arguably more important concept in ecology and evolution, "population," has gone largely unexamined until very recently (e.g., Gannett 2003; Gildenhuys 2009; Millstein 2009a, 2010; Godfrey-Smith 2009; Bouchard 2011). Elsewhere (Millstein 2009a, 2010), I defend a particular characterization of "populations," the Causal Interactionist Population Concept (CIPC), first, through a demonstration that populations are *individuals*[1] and second, by showing how the CIPC illuminates case studies that include populations, metapopulations, and patchy populations of various types. In this paper, I defend the CIPC in a different way; I show its usefulness in addressing a challenging conceptual and methodological issue in biology, namely, how to understand and deploy the concepts of "homogeneous environment" and "heterogeneous environment." Thus, the first half of the paper is not on populations at all, but rather, on environment concepts; as a side benefit, I seek to further our understanding of these as well.

The structure of the paper is as follows. I begin with background of a historical case, "The Great Snail Debate" of the 1950s,[2] and show how during the course of that debate, a disagreement over heterogeneous environments arose. I then consider whether Robert Brandon's or Richard Levins's concepts of "environment" can settle the disagreement; I argue that they cannot do so without further enhancement. I then suggest that we can deploy the concept of "population" to enhance our environment concepts and settle the disagreement. However, the common population-as-deme view is inadequate to the task; I show how the CIPC can succeed where the population-as-deme view fails. Last, I offer some concluding thoughts.

2. Heterogeneous Environments and "The Great Snail Debate" of the 1950s

The focus of The Great Snail Debate was the grove snail, *Cepaea nemoralis*, a land snail that is found throughout Europe and England. It is a highly polymorphic species, and has been so since at least the Pleistocene, both in color (pink, brown, or yellow) and in the number of bands (having anywhere from zero to five visible bands). The snails live in numerous colonies[3] of varying sizes, with some but very little migration between colonies.

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[1] Drawing on the Ghiselin and Hull analysis of species as individuals (Ghiselin 1974, 1997; Hull 1976, 1978, 1980).

[2] Here I provide only a sketch; Millstein (2008, 2009b) gives greater detail. The moniker "Great Snail Debate" is due to Provine (1986).

[3] For the first part of the paper I use the term "colonies" rather than "populations," in part because the disputants often used the term and in part not to beg any questions about what the populations were. Colonies can be understood as groupings of snails geographically

Different colors and different numbers of bands predominate in different colonies; for example, the majority of snails in one colony might be yellow while the majority in a different colony might be pink. Disputants in The Great Snail Debate sought to determine which evolutionary processes accounted for the contemporary colony distributions.

There were two main camps involved in The Great Snail Debate. The first camp, Arthur J. Cain and Philip Sheppard, was studying the snails in England. They argued that the snail distributions were primarily due to selection, with little or no role for random drift. The second camp, Maxime Lamotte, was studying the snails in France. He agreed with Cain and Sheppard that the snail distributions were partially due to selection; however, he argued that there was in fact a *substantial* role for drift. Importantly, however, both camps agreed that there were correlations between snail colors and habitat backgrounds due to visual selection by predator; thrushes would find it harder to spot snails whose colors were similar to that of their background, giving the camouflaged snails an advantage in those environments.

In the course of the debate, Cain and Sheppard criticized Lamotte's inclusion of large colonies in his studies:

> Because backgrounds vary considerably over small distances, and the larger colonies will tend to be spread over larger areas and therefore over more types of background than the smaller ones,[4] it is to be expected that large colonies will tend to be more alike, since *the diverse effects of selection in different parts of each colony will tend to cancel out when the colony is considered as a whole, and in any case will be reduced to a certain extent by gene flow*. Small colonies will tend to be on more homogeneous backgrounds, and will therefore become more diverse by selection. (1954, 110; emphasis added)

In this passage, Cain and Sheppard seem to be suggesting that selection is occurring within *microhabitats*, and that by examining the whole (heterogeneous) environment of a particular colony, one would miss these more localized selection processes. Indeed, Cain and Sheppard stated that they were "avoiding those [localities] where there is a mixture of types of vegetable formations" (1954: 98).

So, Cain and Sheppard seem to have thought that natural selection occurs in homogeneous environments, so that if a colony of snails was in a heterogeneous area, the data from these colonies should *not* be included because the effects of the selective processes in homogeneous microhabitats would average out. Lamotte, however, disagreed; he seems to

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separated from other groupings of snails, with migration between the groupings difficult or impossible.

[4] Lamotte (1959) clarified that the larger areas were no more heterogeneous than the smaller areas; in subsequent publications, Cain and Sheppard changed their critique. However, the issue I want to highlight here is not the evaluation of their data sets, but rather the methodological and conceptual disagreement over heterogeneous environments.

have thought that evolutionary processes could occur across heterogeneous environments, and thus, data from colonies living in heterogeneous areas ought to be included. Homogenous environments, Lamotte asserted, were rare in France; he did his "best to study the populations in all possible environments" (1959: 70-2).

But what does it mean for an environment to be heterogeneous or homogenous? And which is the relevant environment for evolutionary processes?

3. Environment Concepts

3.1. Brandon's Concepts of "Environment"

Robert Brandon has argued for the importance of understanding concepts of environment; as he notes in his co-authored paper with Antonovics and Ellstrand, "for the theory of natural selection to have explanatory power with regard to how adaptations originate, the concept of environment is important as that of fitness" (Antonovics et al. 1988, 280). According to Brandon (1990), we need to distinguish between three different concepts of environment:

1. **external environment** – the sum total of biotic and abiotic factors external to the organisms in question.

   Some of these factors may not affect organisms' fitness or relative fitness, so an external environment can look heterogeneous but be homogeneous *from the organisms' point of view*, which leads to the second concept of environment.

2. **ecological environment** – consists of only those features of the external environment that affect the fitness of a given genotype; organisms "define" their environments. These are **homogeneous** when *fitness values* remain relatively constant across the area.

3. **selective environment** – consists of only those features of the external environment that affect the relative fitnesses of multiple genotypes in an area. These are **homogeneous** when the *relative fitness values* remain relatively constant across the area (at a minimum, homogeneity requires that the ordinal relation of genotypes not change across the area).

Brandon further suggests that organisms that are mobile enough to move between environmental patches are in a *homogeneous* selective environment:

   Moths fly around and land on many different trees. Their probability of being devoured by a bird depends on the match, or lack thereof, of their color and the

statistical average color of the background that they create by their behavior. Thus if the two tree types are distributed randomly about the woods and both types of moths show no behavioral preference for one type of tree over the other, then the woods in question are selectively homogeneous. (2005, 166)

Moreover, Antonovics, Ellstrand, and Brandon argue that, understood properly, selection occurs in homogeneous selective environments[5]:

If we grew one plant on good soil, and another on poor soil, the one on good soil would probably survive better, grow larger, and have more seed. Although we might be tempted to say one plant had a greater 'fitness' than the other, we are in this case referring to properties of the environment rather than to properties of the phenotypes of those plants which would explain their differential success... In other words for the theory of natural selection to have explanatory power, we must compare the fitness of different phenotypes in identical environments. Conversely, two environments can be thought of as homogeneous (with regard to selection) if their effect on the relative fitness of phenotypes is the same. *It is within such selectively homogeneous environments that differential fitness is the result of properties of the organism and within which the theory of natural selection therefore has explanatory power.* (1988, 280; emphasis added)

If Cain and Sheppard held views similar to these, and if they thought that the snails were not very mobile (i.e., not mobile enough to move between environmental patches in some areas), then they would have thought that in some cases the snails were not in homogeneous selective environments. Thus, (again assuming that Cain and Sheppard's views were similar to Brandon's), they would have refused to consider data from colonies in heterogeneous environments, as they indeed did.

3.2. Levins's Concepts of "Environment"

Although many philosophers are familiar with Brandon's concepts of environment, those of Richard Levins (1968) are better known among biologists. Levins classifies environments in evolutionary contexts somewhat differently than Brandon; instead of two categories of selective environment (homogeneous and heterogeneous), there are three:

1. **homogeneous environment -** organisms spend their lives in a uniform environment.

2. **fine-grained heterogeneous environment** - organisms disperse freely among many patches (in space or time) during the course of their lifetime.

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[5] Brandon (1990) and Damuth (1985) make similar arguments.

3. **coarse-grained heterogeneous environment** - organisms spend their lives in one patch.

Note that intermediates between the extremes of "fine-grain" and "coarse-grain" are possible, i.e., organisms may spend their lives in more than one patch, yet not disperse freely enough so that they experience them with a frequency equivalent to that of the environment. However, in many cases the extremes are reasonable approximations, and so in what follows I ignore the possibility of intermediates.

The category of fine-grained heterogeneous environments marks a difference between Brandon's typology and Levins's; recall that such an environment would count as homogeneous for Brandon. That difference is important because certain phenomena may be expected in a fine-grained heterogeneous environment that would not necessarily be expected in a Levins-sense homogeneous one. For example, selection for adaptive plasticity is more likely in a fine-grained environment than it is in one that is Levins-sense homogenous; organisms in fine-grained environments are also more likely to experience constrained geographic ranges if interbreeding inhibits adaptation to environmental extremes (see Table 1). Therefore, the concepts of "fine-grained heterogeneous environment" and "homogeneous environment" should not be collapsed. Levins's typology is superior to that of Brandon's in that respect.

However, Brandon is certainly right to emphasize that *organisms* determine the nature of the selective environment. (Not that Levins would likely disagree; after all, the distinction between fine-grained and coarse-grained is itself organism-centered). Thus, the two typologies might be profitably (but tentatively – I make further refinements below) combined as follows:

1. **homogeneous selective environment** – consists of only those features of the external environment that cause the relative fitnesses of multiple genotypes in an area to remain relatively constant across the area.

2. **fine-grained heterogeneous selective environment** – consists of only those features of the external environment that cause the relative fitnesses of multiple genotypes in an area to vary across the area, where organisms disperse freely among many patches (in space or time) during the course of their lifetime.

3. **coarse-grained heterogeneous selective environment** – consists of only those features of the external environment that cause the relative fitnesses of multiple genotypes in an area to vary across the area, where organisms spend their lives in one patch.

A couple of clarifications here: first, the term "selective environment" should not be taken to

exclude other evolutionary processes from occurring in the same area, drift in particular. Second, speaking of a *heterogeneous* selective environment might seem to be begging the question against Brandon. In section 4.2, I explain why such a locution is sensible and desirable.

3.3. Incompleteness of Environment Concepts

Even by combining the best elements of Levins's and Brandon's concepts, we can't settle the question of which environments to consider in the snail studies because in many cases it will be unclear when we have homogeneous environments and when we have heterogeneous environments. To see this, consider the region shown in Figure 1, consisting of three patch types relevant to the fitness of the organisms (e.g., pink, brown, and yellow snails distributed across pinkish, brownish, and yellow-greenish backgrounds). Suppose the snails only regularly move between *some* patches: between a, b, c, and d; between e, a, and f; and within (but not outside of) g. Now consider three ways of drawing area boundaries:

1. Around each patch individually, so that there are there are seven areas.
2. Around the entire region depicted, so that there is one area.
3. Around b, c, and d, including some of a; around e and f, including some of a; and around g, including some of a.
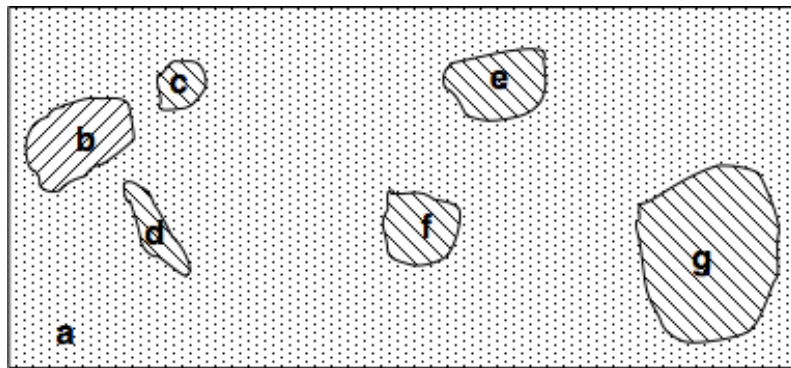

Figure 1: A patchy region. *a* is one patch type (e.g., brownish background), *b* is second patch type (e.g., pinkish background), and *c, d, e, f,* and *g* are a third patch type (e.g., yellow-greenish background).

If the boundaries are drawn the first way, there are seven homogeneous environments. If the boundaries are drawn the second way, there is one coarse-grained heterogeneous environment. If the boundaries are drawn the third way, there are three heterogeneous environments, two of which are fine-grained and one of which is coarse-grained.

This variability in classifying environments as homogenous, coarse-grained heterogeneous, or fine-grained heterogeneous arises because both Levins and Brandon are silent on the question of how one delineates the boundaries of a selective environment. Thus, the Brandon and Levins environment concepts are *incomplete*. They cannot help to settle disputes (like the one between Lamotte and the team of Cain and Sheppard) over which areas to include in one's data set because they are not powerful enough to determine which areas are heterogeneous and in what way. Yet, whether the environments are fine-grained or coarse-grained matters; Table 1 compares the predictions of a fine-grained heterogeneous environment to that of a coarse-grained one.

Table 1
A comparison of selection trajectory predictions (ceteris paribus*)

Fine-grained environments	Coarse-grained environments	Source
Fixation for allele favored on average across patches†	Fixation of locally favored alleles within patches	Spieth (1979)
Monomorphism†	Polymorphism	Levene (1953), Levins and MacArthur (1966), Hedrick et al. (1976)
Single generalist species	Multiple specialized species	Brown and Pavlovic (1992)
Adaptive plasticity	No particular pattern of plasticity (instead, local adaptation)	Levins (1963), Gillespie (1974), Pigliucci et al. (2003), Banta et al. (2007)
Constrained numbers of organisms and geographic range	Increasing numbers of organisms and geographic range	Kirkpatrick and Barton (1997)

* e.g., excluding habitat choice, heterosis.
† unless there is very strong selection to overcome interbreeding; see, e.g., Slatkin (1987).

Consider, for example, the first row of Table 1. If organisms are frequently changing selectively relevant patches in space or time (a fine-grained environment), then even though a trait might be advantageous for an organism in one patch (e.g., a yellow snail in a yellow-greenish background), that same trait might be disadvantageous in another patch (e.g., a yellow snail in a pinkish background). Such a trait might therefore be selected against. The trait that would do best is one that, while it is perhaps not particularly advantageous in any of the patches, is one that is the most favorable on average (or, alternatively, as the fourth row

of the table indicates, an adaptively plastic trait). It is fairly straightforward to see how this might lead to a monomorphic population (second row) with no particular predisposition to speciate (third row); moreover, organisms might have difficulty expanding their numbers outside of the range if the edges of the range are much different from the habitat in the interior (fifth row). On the other hand, if organisms are spending their lives in one patch (a coarse-grained environment), they can more easily adapt to their particular patch, perhaps leading to fixation of the favored allele (first row) and thus, polymorphism, since there are different adaptations within the species (second row). Over time, these polymorphisms might become separate species (third row); however, there is no particular expectation of adaptive plasticity (fourth row) or reason to think that organisms are limited in their numbers or geographic range (fifth row).

In short, Table 1 shows that if boundaries are drawn any way that one chooses, one risks making the wrong predictions because the location of an environment's boundaries affects whether the environment is fine-grained or coarse-grained (as the discussion of Figure 1 shows). Thus, to deploy our environment concepts in a way that preserves our ability to make accurate predictions, we need a principled way to draw the boundaries.

4. The Population Concept Completes the Environment Concepts

My suggestion, consistent with the standard view that it is populations that undergo evolution, is that *populations* dictate the boundaries of the selective environment.[6] More specifically, the boundaries of the environment would be delineated by the fullest extent of the spatial location of the population. To illustrate, consider Figure 1 again. If there were separate populations in each of the seven background patches, then there would be seven separate homogeneous environments. On the other hand, if populations were to occur in more than one background patch, then the environment(s) would be heterogeneous; then, based on the frequency of organisms changing patches in space and time, we could determine whether a given heterogeneous environment is fine-grained or coarse-grained.

Here are four advantages of recognizing that populations bound environments (more later). First, I think this recognition is implicitly assumed in the widely used Levins typology of environments.[7] Second, it follows Brandon's reasonable intuition that environments should be understood relative to the organisms that inhabit them. Third, it avoids the problems of an "anything goes" boundary solution, which would not be consistent with the different predictions in different types of environments shown in Table 1. And fourth, it respects the *types* of predictions of homogeneous environment vs. fine-grained vs. coarse grained; note that these were mostly population-level predictions (e.g., polymorphism, fixation, etc.), and that the predictions reflect the "common fate" experienced by organisms

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[6] See Glymour (2011) and Abrams (2014) for alternate views.

[7] As Templeton and Rothman (1978) note, "Levins and many other authors use grain at the population level" (176).

of the same population.

So, we need a population concept to delineate the environment that organisms are evolving in. But which population concept?

4.1. Population-as-deme

The most common answer among population geneticists is that populations are *demes* – i.e., groups of actively interbreeding organisms of the same species. If we take my suggestion that populations delineate environments together with the population-as-deme view, then the boundaries of the environment would be delineated by the fullest extent of the spatial location of the interbreeding organisms.

However, the population-as-deme view is problematic. To see why, suppose that a population *sensu* deme is spread across a heterogeneous environment with two patches. Suppose further that over time, local adaptation occurs each of the habitat patches, and that over time, organisms in the different patches may differentiate enough so that we would call them different species on some reasonable species concept. (Species that exhibit configurations similar to this include threespine stickleback fish, metal-tolerant grasses, and hawthorn and apple maggots (*Rhagoletis pomonella*)). Under this scenario, there could be significant differentiation between organisms, but unless there were a significant change in *breeding* patterns, there would still only be one population according to the population-as-deme view. Thus, breeding-related differentiation would count (e.g., habitat choice, assortative mating) but non-breeding-related differentiation would not (e.g., differential adaptation), even though both types of differentiation can lead to speciation.

This seems arbitrary and incomplete. Arguably, one aspect of being a population is as a possible precursor to a new species, yet some precursors are not recognized (while others are). The significant differentiation prior to speciation ought to be recognized conceptually, especially since differential adaptation with linkage can limit gene flow. The failure to do so is a flaw of the population-as-deme view.

4.2. The Causal Interactionist Population Concept (CIPC)

The Causal Interactionist Population Concept (CIPC) is an alternative to the population-as-deme view. Details of the view can be found elsewhere (Millstein 2009a, 2010); here I summarize briefly. The CIPC characterizes populations in ecological and evolutionary contexts[8] as consisting of at least two conspecific organisms who, 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

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[8] This qualification recognizes that other areas of study, such as statistics and biomedicine, may have alternative population concepts.

are much higher within the grouping than outside.[9] Both reproductive and survival interactions should be understood broadly; relevant interactions include both unsuccessful and successful matings (interbreeding), offspring rearing, competition for limited resources, and cooperative activities.

Recall the scenario where there was local adaptation within two patches with widespread interbreeding across patches. Now suppose that in addition to reproductive interactions within and between organisms in patches, there were significant survival interaction rates within (but *not* between) patches. Since the rates of causal interactions within patches are significantly greater than the rates of causal interactions more generally, on the CIPC there are two populations (that may later become two species). Thus, there are two homogeneous evolutionary environments whose boundaries are delineated by the spatial range of the causal interactions of the two populations. Since there are some interactions across the two populations, they form a *metapopulation*[10] across a heterogeneous environment (probably, but not necessarily, coarse-grained, if interactions are a good proxy for the movement of organisms through space and time). Therefore the CIPC, unlike the population-as-deme view, preserves the idea that splitting into populations precedes splitting into species. On the other hand, according to the CIPC, if the rates of causal interactions within patches were *not* significantly greater than the rates of causal interactions more generally, then there would be only one population evolving in a heterogeneous environment (probably, but not necessarily, fine-grained – again, it would depend on the movement of organisms through space and time).

Note that using the CIPC (or the population-as-deme view, for that matter) to delineate the boundaries of the selective environment entails that selection can occur across a heterogeneous environment, contra the view of Brandon and others that selection should be understood within homogeneous environments only. Indeed, the authors cited in Table 1 suggest that thinking of selection occurring across heterogeneous environments is widespread. But is it legitimate? Recall that on Brandon's view, fine-grained heterogeneous environments are considered homogenous, so it is only the coarse-grained ones that are controversial. Brandon handles the latter type of case by calling selection within a selectively homogeneous environment *simple natural selection*, whereas selection in coarse-grained environments is *compound natural selection* – "a process consisting of natural selection within environments and distribution into environments" (1990, 73). For example, suppose the pollen and seeds of two plant genotypes are randomly distributed across two habitat

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[9] Here I draw on Simon (2002).

[10] According to the Causal Interactionist Metapopulation Concept, metapopulations consist of at least two local populations (as characterized above) of the same species, linked by migration or dispersal, such that organisms occasionally change which population they are a part of; rates of interaction within local populations are much higher than the rates of interaction among local populations (Millstein 2010).

patches, one where the soil contains heavy metals and one where it does not.[11] On Brandon's view, the distribution forms the first part of the process of compound natural selection. Then suppose that there is selection within each of the environmental patches, with one genotype being favored in the soil that contains heavy metals and the other genotype being favored in the soil that does not contain heavy metal. The selection within these two environments is the second part of the process, according to Brandon. So, although Brandon does speak of selection within heterogeneous environments, in truth on his account the *selection* part of compound natural selection is occurring within homogeneous selective environments; only the *distribution* occurs across heterogeneous environments.

However, there are reasons to think that selection itself can occur across heterogeneous environments, as using the CIPC as an environment delineator would imply. Consider (as Brandon would readily acknowledge) that there are reproductive interactions occurring across the habitat patches. In addition, there are likely to be survival interactions occurring across patches, particularly between plants who are near the borderline between the two patches; for example, the plants on different sides of the patch will probably be competing for water, for nutrients in the soil, for light, for root space. Even if two plants on different sides of the border are not competing directly, they may be affected by the competition between the plants that are the border, meaning that because of those near-border competitions there is more or less water available for them, more or fewer nutrients, etc. These sorts of survival interactions – examples of Darwin's "struggle for existence" – are part of the process of natural selection. It thus does not make sense, in situations such as those described here, to say that there two separate selection processes when in fact all of the organisms in both patches are engaged in a struggle for existence and in reproductive interactions (also part of natural selection) with one another. Of course, it is also possible that there are cases where few or no interactions occur across patches, or where those interactions were very much fewer than the interactions within the patches; in those cases, there *would* be two separate selection processes going on in two separate environments. These considerations vindicate the CIPC approach to environment delineation.[12]

Furthermore, unlike the population-as-deme view, the CIPC helps us understand debates like The Great Snail Debate. Recall that Cain and Sheppard disagreed with Lamotte over the relevant type of environment for evolutionary processes. Cain and Sheppard thought that each individual patch within the area is its own (homogenous) environment, and that these should be studied separately, whereas Lamotte thought that one heterogeneous area as a whole characterizes the environment. If the rates of interactions within patches were much higher than the rates of interactions between patches, then in a sense both camps were right.

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[11] This example is modified from one that Brandon describes later in his book, drawn from the work of Antonovics et al. (1971).

[12] Note that similar considerations apply to understanding drift across heterogeneous environments and that the delineation via populations would therefore be the same as for selection.

Cain and Sheppard's view would let us study the dynamics of the *populations*, while Lamotte's view would let us study the dynamics of the *metapopulation*. However, if the rates of interactions were more or less consistent across patches, then Lamotte was right. We should study a colony's entire heterogeneous environment.

5. Conclusions

I have argued that we ought to characterize our environment concepts as described in Section 3.2 with the CIPC-based delineations specified in Section 4.2. When trying to understand the evolution of organisms spread over heterogeneous areas, the CIPC directs us to, first, pay attention to the interactions of organisms across the landscape; second, identify the fullest extent of the densest pockets of survival and reproductive interactions – i.e., the populations, and third, delineate the environments based on the geographic range of the populations. Once that is done, we can determine whether the environments are homogeneous or heterogeneous, and if heterogeneous, whether coarse-grained or fine-grained (based on the dispersal abilities of the organisms). We can then determine the appropriate models to apply to our study populations.

The case for a population concept in evolutionary and ecological contexts, and the Causal Interactionist Population Concept (CIPC) more specifically, now rests on 1) a demonstration that populations are *individuals* (Millstein 2009a); 2) an illustration of how the CIPC illuminates a variety of different population structures (continuous populations, metapopulations, patchy populations, etc.) for a variety of species[13] (Millstein 2010); and 3) an argument that the CIPC is required for understanding and deploying concepts of homogeneous and heterogeneous environment (this paper). Furthermore, the discussion above hints at other roles for the CIPC to play. Since selection in heterogeneous environments is thought to be one mechanism through which sympatric speciation can occur, the CIPC may help clarify this somewhat controversial process by elucidating the separation of populations prior to the separation of species. In addition, since the 1950s many other processes have been proposed to explain the distributions of the *Cepaea nemoralis* populations, including repeated extinction and recolonization of habitat patches (Cameron and Pannett 1985, Cameron 2001), founder effects (Cameron and Dillon 1984), and rare, long distance migrations (Davison 2000); a robust population concept like the CIPC would seem to be relevant to each of these phenomena. However, these are topics for another day.

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[13] The case studies include *Linanthus parryae* (desert snow, a flowering plant), *Pseudomonas* (bacteria), *Chrysomela aeneicollis* (montane willow leaf beetle), *Eubalaena australis* (Southern Ocean right whale), and *Gasterosteus aculeatus* (threespine stickleback fish). In other words, not just land snails.

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