

Exploring the Status of Population Genetics: The Role of Ecology

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Abstract The status of population genetics has become hotly debated among biologists and philosophers of biology. Many seem to view population genetics as relatively unchanged since the Modern Synthesis and have argued that subjects such as development were left out of the Synthesis. Some have called for an extended evolutionary synthesis or for recognizing the insignificance of population genetics. Yet others such as Michael Lynch have defended population genetics, declaring “nothing in evolution makes sense except in the light of population genetics” (a twist on Dobzhansky’s famous slogan that “nothing in biology makes sense except in the light of evolution”). Missing from this discussion is the use of population genetics to shed light on ecology and vice versa, beginning in the 1940s and continuing until the present day. I highlight some of that history through an overview of traditions such as ecological genetics and population biology, followed by a slightly more in-depth look at a contemporary study of the endangered California Tiger Salamander. I argue that population genetics is a powerful and useful tool that continues to be used and modified, even if it isn’t required for all evolutionary explanations or doesn’t incorporate all the causal factors of evolution.

Keywords California Tiger Salamander · Ecology · Ecological genetics · Evolution · Modern Synthesis · Population biology · Population genetics

The status of population genetics has been debated recently among biologists and philosophers of biology. Much of the debate has surrounded topics that were purportedly left out of the Modern Synthesis, such as development. Some authors have called for reducing the status of population genetics in evolutionary theory, or for radical revisions (“critics”). Other authors have defended the status of population genetics, perhaps as a “cornerstone” or “backbone” of evolutionary theory (“supporters”). And, of course, still other authors have taken a position in between these two (“middle ground”).

A brief sampling of these three positions follows. First, here are some critics of population genetics:

It is now approximately half a century since the neo-Darwinian synthesis was formulated.... Yet the successes of the theory are limited to the interpretation of the minutiae of evolution, such as the adaptive change in coloration of moths. (Ho and Saunders 1979, p. 589)

Models of genetic changes in populations do not provide us with much illumination of the ways in which populations evolve. (Dupré 1993, p. 138)

...millions of biology students have been taught the view (from population genetics) that “evolution is change in gene frequencies.” Isn’t that an inspiring theme? This view forces the explanation toward mathematics and abstract descriptions of genes, and away from butterflies and zebras, or Australopithecines and Neanderthals. (Carroll 2006, p. 294)

Here are some supporters of population genetics:

Population genetics is the cornerstone of modern evolutionary biology. (Michod 1981, p. 2)

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The science of population genetics is the auto mechanics of evolutionary biology. (Lewontin 2000, p. 5)¹

Nothing in evolution makes sense except in the light of population genetics. (Lynch 2007, p. 8598)

Finally, here are some authors offering a middle ground:

Few sensible biologists would deny that the population genetic framework is essential to evolutionary biology.... But to require a population genetic approach to all questions in evolutionary biology seems too stringent a criterion for determining what is a convincing hypothesis. (Bromham 2009, p. 399)

I think that while population genetics is an important part of evolutionary theory, it is an error and a gross simplification to see evolution as fundamentally a matter of changes in gene frequencies over time. (Pigliucci 2008, p. 317)

Much of my own work has its origins in population genetics (e.g., Millstein 2002; Millstein and Skipper 2007; Millstein et al. 2009). So, I might appear to fall in the “supporter” category. However, I am much more comfortable in the middle ground. I think that both Bromham’s and Pigliucci’s points are well taken. In support of the former point, one need only consider some of the excellent comparative studies in paleontology to see that population genetics is not required for (indeed, would be impossible to apply to) *all* evolutionary questions—and one can accept this while still believing that population genetics is essential to evolutionary biology as a whole. In support of the latter point, as many other authors have suggested, consideration of the importance of phenomena such as adaptation and speciation, let alone development, are sufficient to show that there is more to evolution than changes in gene frequencies over time. The critics, however, go too far. As I shall argue in this article, the successes of population genetics go far beyond “the interpretation of the minutiae of evolution,” the models of population genetics do illuminate a great deal about the ways that populations evolve, and population genetics need not focus our attention towards mathematics and genes and away from the organisms themselves.

Indeed, I think one comes to such conclusions only by making two false assumptions: (1) Population genetics can be completely understood as a purely *abstract* set of mathematical models (as are typically found in population

¹ Note that Lewontin, in the essay from which this quote is taken and elsewhere, is quick to point out the limitations of population genetics. Also, although the “auto mechanics” comment is a bit cryptic, it can be reasonably interpreted as meaning “that which gets things going.” Judging by Lewontin’s practice, if not always his stated views, Lewontin is a supporter of population genetics, albeit not as staunch as some.

genetics and related textbooks)—nothing more. (2) Population genetics is a product of the Modern Synthesis period, generally dated to 1930–1950 (approximately); its models have remained essentially *unchanged* since then. Interestingly, it is not just the critics who make these false assumptions; these are widespread (albeit not universal) assumptions made by critics *and* supporters, as well as those in between. I will use Pigliucci, who I have categorized as belonging to the middle-ground camp, as an illustration, mainly because he is explicit about views that are implicit in many other authors. With respect to the first assumption, as I noted earlier, much focus has been on the claim that development was left out of the Synthesis. But Pigliucci claims:

Less well understood is the equally puzzling fact that *the Modern Synthesis basically ignored ecology* (despite a strong research program in evolutionary ecology), so much so that ecologists and evolutionary biologists now hardly talk to each other, and we have no organic theory of how community and ecosystems ecology are connected to evolutionary biology. (Pigliucci 2009, p. 136; emphasis added)

If we think that population genetics has had little or no contact with the ecology of natural populations—if we think that population genetics is purely theoretical—then we will tend to see it as an abstract set of mathematical models with little relevance to much of anything. So, if the first assumption were correct, we ought to be swayed away from the supporters’ position and towards the critics’ position (perhaps even more so than Pigliucci himself). We might even be persuaded to go as far as Dupré (1993, p. 141), who asserts that “practical benefits neither have been delivered nor, even by the most ardent enthusiasts for population genetics, are they anticipated.”

With respect to the second assumption, Pigliucci states:

There is much talk these days of the possibility that the Modern Synthesis, the current conceptual framework in evolutionary biology, is due for a makeover.... This is ruffling quite a few feathers, though it should not really be surprising that a theory proposed in the 1930s and 1940s—before the discovery of the structure of DNA, not to mention genomics and evo-devo—may be a bit out of date. (Pigliucci 2009, p. 134)²

I believe that Pigliucci and others who make implicit and explicit claims such as these would acknowledge that in general, theories change over time. I think they would even acknowledge certain types of changes to the models of

² Okasha (2008) is even more explicit: “The basic structure of population-genetic theory has changed little since the days of Fisher, Haldane and Wright.”

population genetics, perhaps that they have incorporated more parameters or insights from molecular studies. Yet for some reason many *talk* about population genetics as though it hasn't changed much—as though it is practically synonymous with the Modern Synthesis. Is population genetics an exception to the general rule that theories change, often dramatically, over time?

I think that the assumptions that population genetics is (1) purely abstract and (2) essentially unchanged since the end of the Modern Synthesis are mistaken. Furthermore, I think we can't really evaluate the status of population genetics today until we see why these assumptions are mistaken. In particular, I want to highlight the *ongoing* and *mutually informative* relationship that ecology has had with population genetics, a relationship that demonstrates the falsity of these assumptions.³ I think that this relationship has been overlooked or downplayed by the majority of those who have participated in the recent debate over the status of population genetics—critics, supporters, and middle ground alike. My primary goal in this article, then, is *not* to settle this debate (that is, I am not seeking to defend my middle-ground position), but rather to suggest that one *cannot* settle the debate without a more complete picture of what population genetics is—a picture that incorporates the ways in which population genetics has intersected with ecology.

In order to examine the intersections between population genetics and ecology, I will provide a brief and fairly potted overview⁴ of the history of the two fields, following different strands (ecological genetics, population biology, and some more contemporary incarnations) where the two fields come together.⁵ This will include a brief overview of where the connection between the two fields stands today and a slightly more in-depth look at recent studies that integrate population genetics and ecology. I will limit my

³ Lloyd (1988) articulates a confirmatory relationship between population genetics and ecology. Nothing I say here is meant to overturn her claims; instead, I mean only to describe an additional sort of relationship.

⁴ That is, I will be leaving out discussion of, and citations to, much good work. To cover it all is a book(s) length project.

⁵ Here it might be objected that neither of these is considered to be “real” ecology by ecologists. Personally, I have little taste for intra-disciplinary disputes about what counts as “real x” (for example, philosophers are often quick to dismiss other work because it does not count as “real philosophy”) and I tend to see them as more turf-protecting than substantive. Here I will just note that my claim is not that *all* aspects of ecology have been incorporated into population genetics, but rather just that *some* aspects have been. Moreover, I suspect that many population geneticists might not recognize these areas as “real” population genetics either. It would not be surprising if blended fields were not fully embraced by those at the core of each of the fields involved in the blend.

⁶ For more, see, e.g., Kingsland (1985), Collins (1986), and Odenbaugh (2006).

discussion to connections between ecology and *population genetics*, even though there are many interesting intersections between ecology and *evolution* more generally (Collins 2011 discussed this topic). I will conclude with some general implications for our views about theories and about population genetics in particular.

Even though I have circumscribed the domain of this paper, there will no doubt still be controversy over what counts as “population genetics,” what counts as “ecology,” and what counts as an intersection (Gerson 2007) between the two. Indeed, this is a point that I also wish to make: over time, as population genetics has been practiced by different research groups, it has changed in many different directions and overlapped with many different disciplines, so that the boundaries between population genetics theory and ecological theory are no longer clear-cut (which is not to say that the fields are fully integrated). Roughly, though, population genetics might be taken to be: (1) models that assume that evolution is change in gene/genotype frequencies over time; (2) models that have their roots in Hardy–Weinberg equilibrium (and thus in Mendelian factor behavior), generally taken to be one-locus, two-allele models; or (3) models that track or infer frequency changes in genotypes and phenotypes⁷ over time, and the way that various evolutionary mechanisms affect those changes. The third is the broadest understanding of the three, and it is the one that I myself hold. (The first, in my view, is a claim that one might make about the models of population genetics, rather than a claim embodied by the models themselves. That is, one might believe that evolution is essentially gene/genotype frequencies over time, but mere use of the models does not imply that belief, since one might simply believe that the models were tracking one type of evolution or one aspect of evolution.)

One Strand of Population Genetics and Ecology: *Ecological Genetics*

Ecological Genetics of the 1940s and 1950s

There is perhaps no better characterization of *ecological genetics* than that given by its founder, E. B. Ford:

It is a surprising fact that evolution, the fundamental concept of biology, has rarely been studied in wild

⁷ Here it might be objected that population genetics tracks only genotypes, not phenotypes. Below, however, we shall see some cases where population genetics models have in fact been used to track changes in phenotype frequencies over time. Of course, one of the criticisms made by proponents of EvoDevo still holds, namely that population genetics ignores the processes through which phenotypes develop out of genotypes.

populations by the fundamental techniques of science, those of *observation and experiment*. Consequently, the process has seldom been detected and analyzed in action. However, I have for many years attempted to remedy that omission by a method which has in fact proved effective: *one which combines fieldwork and laboratory genetics....* The fieldwork needed in these investigations is of several kinds. It involves detailed observation...having strict regard to the ecology of the habitats. Also it often requires long-continued estimates of the frequency of genes or of characters controlled on a polygenic or a multi-factorial basis. (Ford 1964, p. 1; emphasis added)

A number of well-known studies were done in this vein (including Ford's own 1940 "Genetic research in the Lepidoptera") in the 1940s and the 1950s, i.e., during and immediately following the Synthesis. Perhaps the best known of those considered in the tradition of Ford's "school" of ecological genetics are the studies of *Biston betularia* (peppered moth) by Kettlewell (1955, 1956), the studies of *Cepaea nemoralis* (grove snail) by Cain and Sheppard (1950, 1954), and the studies of *Panaxia dominula* (scarlet tiger moth) by Fisher and Ford (1947).

However, there are a number of other, equally well-known studies during this time period that are *not* part of the Fordian tradition but that fit Ford's characterization of ecological genetics. That is, they combine observation and experiment, fieldwork and laboratory genetics, with strict regard to the ecology of habitats, in order to study evolution in wild populations. These studies include Sewall Wright, Theodosius Dobzhansky, and Carl Epling's (1942, 1943) studies of *Linanthus parryae* (desert snow), Maxime Lamotte's (1951, 1959) studies of *Cepaea nemoralis*, and Wright's (1948) studies of *Panaxia dominula*. I think it is fair to say that one of the primary differences between those who were truly in Ford's tradition and those who were not is the former's commitment to an adaptationist approach to evolution; however, as I have argued in particular with respect to the studies of *Cepaea nemoralis* (Millstein 2008, 2009), they in fact shared many techniques and assumptions.

The ecological genetics of this time period can be roughly characterized as follows. It required detailed knowledge of the organism under study and its habitat, including climate and interactions with other organisms, particularly predator/prey. Visible phenotypic traits were studied, with information about underlying genetics often inferred. (For example, Cain and Sheppard stated that work needed to be done on the genetics of *Cepaea nemoralis*, but that it appeared that they were dealing with two sets of genes—one controlling color and one controlling banding—with linkages of "varying degrees of closeness" (1950, p. 287), and they proceeded on those assumptions, assumptions that were later confirmed.) Studies

were performed across multiple generations, tracking evolutionary processes in the short term. Biologists used population-genetic equations to help determine which evolutionary processes were at work (particularly selection and drift) and to what extent (for example, Lamotte's study of *Cepaea nemoralis* used Wright's population genetics equations to show that the variance between small populations and large populations were consistent with the expectations of random drift). Key ecological variables of abundance ("population size") and distribution (which types located where) were estimated using techniques such as mark, release, and recapture.

Importantly, the ecological genetics (understood broadly, as outlined here) of this time period exemplifies how ecology can influence population genetics and vice versa. Some biologists emerged from this time period convinced that it is primarily selection that governs the changes in the distributions of phenotypic traits over time, whereas others were convinced that multiple types of evolutionary processes govern those changes. This mixed lesson set the stage for later debates over the neutral theory.⁸ There was agreement, however, that in-depth knowledge of organisms in their habitats is essential for understanding whether selection is operating and what type of selection (selection by predator, climatic selection, etc.) is present, on which traits, in conjunction with which causal factors, whether biotic or abiotic. The studies showed convincingly that selection and other evolutionary processes occur at ecological time scales and that ecological variables such as abundance and distribution affect evolutionary processes (e.g., selection versus drift), and those processes in turn affect abundance and distribution. Finally, they showed that inter-species relationships (e.g., predator/prey) might matter for both ecology and evolution. These insights were not always fully appreciated, however; for example, rather than seeing that ecological and evolutionary time scales are commensurate, Slobodkin (1961) famously distinguished between "ecological time" (about ten generations) and "evolutionary time" (on the order of one-half million years).

Ecological Genetics Today

Sara Via sees the roots of her work and the work of other contemporary biologists in that of E. B. Ford's, although of course ecological genetics has not remained static:

Despite many changes in techniques, several constants have emerged in ecological genetics as an approach to the study of evolution. First, the focus is

⁸ For elaboration of this point, see "The Origins of the Neutralist-Selectionist Debates," a transcript of a discussion involving John Beatty, James Crow, Michael Dietrich, and Richard Lewontin (http://authors.library.caltech.edu/5456/1/hrst.mit.edu/hrs/evolution/public/transcripts/origins_transcript.html).

on the *genetics of ecologically important phenotypic traits* that affect organisms' interactions with their biotic and abiotic environments. These are the *traits that become adaptations under natural selection* and that may also lead to preexisting reproductive isolation. Next, ecological genetics is an *experimental approach*, with a focus on *natural populations rather than on model systems*. Finally, field studies of both genetic variability and natural selection have always been central to ecological genetics. (Via 2002, pp. S1–S2; emphasis added)

Indeed, ecological genetics is alive and well. The Ecological Genetics Group is a special interest group of the British Ecological Society and the Genetics Society. Programs explicitly specializing in ecological genetics can be found at places such as the University of Helsinki, Michigan State University, and New Mexico State University. Many more universities offer courses in ecological genetics. Below, I will discuss a contemporary case of ecological genetics in more detail.

Another Strand of Population Genetics and Ecology: Population Biology

Population Biology of the 1960s

According to Jay Odenbaugh:

In the 1960s, [Richard] Levins, Richard Lewontin, Robert MacArthur, E. O. Wilson, Leigh Van Valen, and others were interested in integrating different areas of population biology mathematically. Apparently they met on several occasions at the MacArthur's lakeside home in Marlboro, Vermont discussing their own work in population genetics, ecology, biogeography, and ethology and how a "simple theory" might be devised. (Odenbaugh 2006, p. 608)

Odenbaugh (p. 609) contends "that Levins' 1966 essay is a methodological statement and defense of this research program," i.e., population biology. Levins first characterizes population genetics and population ecology, and then shows how population biology seeks to take on the projects of both:

For *population genetics*, a population is specified by the frequencies of genotypes without reference to the age distribution, physiological state as a reflection of past history, or population density. A single population or species is treated at a time, and evolution is usually assumed to occur in a constant environment. *Population ecology*, on the other hand, recognizes multispecies systems, describes populations in terms

of their age distributions, physiological states, and densities. The environment is allowed to vary but the species are treated as genetically homogeneous, so that evolution is ignored.

But there is increasing evidence that demographic time and evolutionary time are commensurate. Thus, *population biology* must deal simultaneously with genetic, physiological, and age heterogeneity within species of multispecies systems changing demographically and evolving under the fluctuating influences of other species in a heterogeneous environment. (Levins 1966, p. 421; emphasis added)

However, Levins (p. 431) famously concluded that one model could not cover all of population biology: "Thus, a satisfactory theory is usually a cluster of models." The population biologists of this time period developed models of environmental heterogeneity (Levins 1968); density-dependent selection (MacArthur 1962, 1965; Lewontin 1965); limiting similarity, convergence and divergence of coexisting species (MacArthur and Levins 1967); and equilibrium island biogeography (MacArthur and Wilson 1967).

As with ecological genetics, the population biology of this time period illustrates the way that ecology can influence (and has influenced) population genetics and vice versa. Whereas ecological genetics showed that *ecological fieldwork* could be integrated with population genetics, population biology showed that *mathematical models* of population genetics and ecology could be integrated.⁹ Other lessons from population biology include the following: In order to deal with the complexity of the systems under study in conjunction with human limitations, tradeoffs between generality, realism, and precision need to be made. Factors such as environmental heterogeneity affect the evolution of populations, which in turn affects ecological parameters such as niche breadth¹⁰ (contra Ho and Saunders, quoted above, who said that population genetics only sheds light on characteristics such as changes in coloration of moths). Simplifications made by population genetics models, such as holding fitness constant or limiting study to one species, can make a significant quantitative difference in some cases (as can ignoring short-term evolution in ecology)—this can either illuminate shortcomings of existing models or show that their simplifications are unproblematic, depending on whether the

⁹ The distinction between "ecological genetics" as involving ecological fieldwork and "population biology" as involving mathematical modeling that I am drawing here is not a strong one, i.e., I am not confident that those terms are consistently used in that way by contemporary biologists. But it appears that originally the terms had those connotations.

¹⁰ Levins (1966) shows how different population biology models "all converge in supporting the theorem that environmental uncertainty leads to increased niche breadth" (pp. 426–427). One of the models is a "simple genetic model with one locus and two alleles" and draws on insights from R.A. Fisher (p. 425).

simplification in question does or does not make a significant difference to the predicted outcome. (Either way, something important is learned.) Finally, it became clear that metapopulations—understanding population structure, or the interactions of organisms across space and time—are important for understanding evolutionary changes over time.

Population Biology Today

In his textbook *Population Biology: Concepts and Models*, Alan Hastings identifies several areas where the interface between ecology and population genetics has “produced fruitful insights” (1997, p. 44):

- (1) Optimization concepts in ecology, where behavior of organisms is assumed to be optimal, e.g., by identifying circumstances under which natural selection can be expected to produce optimal traits;
- (2) Co-evolution, e.g., joint evolution of predator/prey, host/parasitoid, or plant/pollinator; and
- (3) Speciation, e.g., Orr’s (1995) model of speciation as the accumulation of genic incompatibilities between diverging populations (see also Via 2002).

In short, the interface between ecology and population genetics has produced insights into concepts that are central to both ecology and evolution.

Rama Singh and Marcy Uyenoyama’s edited volume *The Evolution of Population Biology* might be one measure of where population biology stands today. It begins with essays by Lewontin and Levins that outline the project of population biology, followed by essays by renowned experts in the field that are meant to show how population biology has been carried out in practice. Topics range from the characterization of the genomic response of an individual in its environment to analysis of biotic and abiotic causes of balancing selection to the role of hybrid zones as an evolutionary force to the evolution of age-dependent fertility and mortality structures. Yet Lewontin and Levins state very clearly that they do not think that their vision has been fulfilled. The editors also admit that “the efforts of numerous scientists who view themselves as population biologists” have not succeeded in “realizing the Lewontin/Levins vision of a population biology that integrates interactions at all levels of organization” (Singh and Uyenoyama 2009, p. 3). However, they suggest that “development of the field was not so much abandoned as postponed” and that the “pervasion of the molecular revolution throughout evolutionary biology” will allow interactions among levels of organization to be explored in depth, with the essays showing how population biology has been brought to the “threshold of full realization” (Singh and Uyenoyama 2009, p. 3). Of course, such a contention will be controversial, but I think it is undeniable that

progress has been made even while acknowledging that the goal has not yet been obtained. Moreover, progress has been made in population biology topics not explored in the volume, such as the evolution and maintenance of meta-population structures. My point here is simply the modest one that good work has been done in population biology and that the quest persists in places such as the journal *Theoretical Population Biology*.

Some Other Strands of Population Genetics and Ecology

Above, I gave a brief overview of two different strands of biological practice where ecology and population genetics come together, namely ecological genetics and population biology. However, there are many other strands (some very recent) where ecology and population genetics have intersected.

Joan Roughgarden’s classic and influential 1979 textbook, *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (reprinted in 1996) includes topics such as evolution in spatially and temporally varying environments, density-dependent natural selection, competition, and predation. Like population biology, Roughgarden’s textbook takes a mathematical approach towards synthesizing population genetics and ecology.¹¹ Indeed, the preface to the original 1979 edition seems to suggest that evolutionary ecology is an outgrowth of population biology: “Theoretical population biology is not a new field although its current visibility is unprecedented.... What is truly recent is the beginnings of a union of population genetic theory with the theory of population ecology” (Roughgarden 1996, p. vii). As Roughgarden notes in the preface to the reprint, however, “evolutionary ecology” has since gone beyond the point where “combining ecological theory with evolutionary theory boiled down to developing models for the simultaneous change of gene frequency and population size” and now includes topics such as game theory and models derived from the behavior and physiology of organisms, which are not derived from population genetics in the same way that the models of Roughgarden’s textbook are.

Roughgarden (personal communication, July 2011), however, objects to my characterization of her textbook as a significant force in bringing together population genetics and ecology, saying that her textbook was as popular as it was not because population geneticists accepted the importance of ecology to their field, but because the parts of the textbook that covered traditional population genetics

¹¹ Other work in this vein, and from around the same time period, includes that of León (1974) and Slatkin and Maynard Smith (1979).

topics did so with a clear exposition,¹² and that some population geneticists go so far as to deny that density- and frequency-dependence are part of population genetics. In short, she questions how prevalent integrations between population genetics and ecology are. Surely she is right that some population geneticists construe their field very narrowly, making it look as though there are very few intersections between ecology and population genetics, but even if that is true it does not overturn my claims in this paper. I am not trying to show that intersections between population genetics and ecology form a majority of either field, which would require a very different sort of analysis than I am offering here; instead, I am trying to show that there is a lot of good work that has been done and continues to be done by well-known and influential people, and to suggest that we ought to pay attention to it.

In addition to the general kind of approach exemplified by Roughgarden's textbook, many intersections between ecology and population genetics show increasing specialization in different areas of ecology. Here is a brief outline of some of the strands (again, with the understanding that these are not meant to be entirely distinct from one another):

Conservation Genetics: Conservation genetics is often traced to the work of Soulé in the 1980s, with Lande's (1988) work seen as a landmark in the field. According to the journal *Conservation Genetics*, the field "focuses on the conservation of genetic diversity and in general, the application of genetic methods towards resolving problems in conservation."

Community Genetics: Antonovics (1992) seeks to examine the "evolutionary genetic processes that occur among interacting populations in communities," realizing that most ecological systems do not involve simple pairwise interactions among species, but multiple complex interactions within and among trophic levels. A recent commentary by Wade (2003) reviews some of the groundwork of the field (e.g., Goodnight 1991) and describes two approaches to community genetics, one due to Whitham et al. (2003) emphasizing the community-shaping effect of genetic variation in keystone species, the other due to Neuhauser et al. (2003), emphasizing strong selection in nonequilibrium, genetically subdivided communities.

Niche Construction: Odling-Smee et al. (2003) propose a two-locus model, with alleles at one locus yielding a phenotype that affects the amount of a key resource in the environment and with the amount of the resource influencing the contribution to fitness of genotypes at a second

locus. Their book laid the groundwork for subsequent progress in the field.

Landscape Genetics: Landscape genetics was initially defined simply as an "amalgamation of molecular population genetics and landscape ecology" with the aim of providing "information about the interaction between landscape features and microevolutionary processes, such as gene flow, genetic drift, and selection" (Manel et al. 2003, p. 189). It has more recently been defined as "research that explicitly quantifies the effects of landscape composition, configuration and matrix quality on gene flow and spatial genetic variation" (Storfer et al. 2006; see Storfer et al. 2010 for a review of recent work in this area). **Ecosystem Genetics:** Ecosystem genetics has recently been characterized as the "study of the genetic interactions that occur between species and their abiotic environment in complex communities" (Whitham et al. 2006; their paper reviews recent work in this area). This is an emerging field. For example: "At the 2011 International Botanical Congress in Melbourne, Australia, a symposium entitled, 'Community and ecosystem genetics: the extended genetic effects of plant species', examined new research in the field of community and ecosystem genetics. Talks focused on: links between contemporary ecological interactions and historic evolutionary dynamics; the role of feedbacks as mechanisms in driving patterns of biodiversity and ecosystem function; and application of these approaches to management and conservation issues as they relate to global change" (Bailey et al. 2012, p. 24).

Elaborating on each of these would be a large undertaking. Instead, to get the general flavor of this sort of work, let's take a look at case studies that exhibit characteristics of traditional ecological genetics as well as contemporary conservation genetics and landscape genetics. Again, this will show the ways in which population genetics has been modified by ecology (and vice versa) and the ways in which it has been found useful by practitioners. There are many such studies that I could describe, and I apologize for not citing them; this is meant to be illustrative.

Studying the California Tiger Salamander (and the Barred Tiger Salamander)

I will focus on two studies of the California Tiger Salamander (CTS) and the Barred Tiger Salamander (BTS) done by Brad Shaffer's lab group at the University of California, Davis,¹³ studies that combine ecology and population genetics. However, it's important to note that the group has done many other studies of the CTS,

¹² I agree with Roughgarden that the textbook is very clear, as well as being better than most in laying out key concepts and assumptions!

¹³ Shaffer is now at the University of California, Los Angeles.

including laboratory studies of their genetics and development, more purely ecological/conservation biology studies of the movements and habits of the salamanders, etc. Thus, it's really best to see the ecology/population genetics studies as one important component of a multi-faceted study of the CTS and its interactions with the BTS.

Before describing the studies, however, we first need a bit of background. There are fourteen species of tiger salamanders across North America. Several populations of the CTS are listed as endangered under the U.S. Endangered Species Act. Temporary vernal pools are breeding grounds for the CTS, though they spend much of their lives on land. The BTS, on the other hand, originates in Texas and the southwestern US. They attain larger size prior to metamorphosis and can be available further into the summer than native CTS, and thus make better live bait for large “trophy” bass. Because of their value as bait, in the 1940s and 1950s bait dealers from the Salinas Valley imported thousands of BTS larvae into California. CTS and BTS had been allopatric for ca 5 million years, but surprisingly, they can hybridize. They have been doing so in some areas of California for an estimated 15–30 generations.

The most obvious ecological difference between the two species is that whereas CTS *always metamorphose* from a juvenile aquatic form to an adult land-dwelling form, BTS exhibits *facultative paedomorphosis*, i.e., it may (or may not) retain juvenile aquatic characteristics. Paedomorphosis is generally regarded as an adaptation for permanent aquatic habitats, because paedomorphs can breed earlier, and generally attain larger body size, larger clutches sizes for females, and possibly greater mating success for males.

“Environment-Dependent Admixture Dynamics in a Tiger Salamander Hybrid Zone”

Fitzpatrick and Shaffer (2004) compare CTS/BTS hybrids in three pool types: vernal pools, human-made ephemeral pools, and perennial pools, studying eight loci and four of each pond type, looking for departures from Hardy-Weinberg equilibrium (HWE) and differences in the distributions of alleles between ponds. They find that seven of the twelve ponds deviated significantly from HWE expectations using all eight markers. They also find a preponderance of non-native alleles in perennial ponds, despite physical distances between ponds that are within the migration capability of the salamanders. They conclude that the salamanders seem to form a mosaic hybrid zone, with different selection pressures in perennial vs. ephemeral ponds. But is this a legitimate conclusion?

Pigliucci and Kaplan (2006), citing Hartl and Clark’s population genetics textbook, point out that *many* factors can cause a departure from HWE: overlapping generations, non-random mating, small population size, migration, etc.

They suggest that this can “complicate (and often make impossible) a straightforward conclusion,” that “additional lines of evidence will be needed,” but that they are “seldom provided” (2006, pp. 247–248).

However, population geneticists who integrate ecology with population genetics are well equipped to address the well-known limitations of HWE analysis. For example, Fitzpatrick and Shaffer sample the spring young-of-the-year larvae so that overlapping generations and immigration are not an issue. They acknowledge that small population size (and thus drift) may be a factor, and emphasize the need for replicating their studies; they acknowledge that observed variation *within* pond types is probably due to drift. Moreover, they address the issue of non-random mating by stating that even though two of the three marker-specific deviations from HWE are habitat-specific, breeding is not likely to be habitat dependent given what else is known about the interactions between tiger salamanders and their habitats.¹⁴ That their conclusions are qualified should not concern us; as those who study science know well, no conclusion is ever definitive, and all are open to being overturned with new evidence.

Pigliucci and Kaplan emphasize the need to find the causes underlying the statistics (a point on which we agree), suggesting that too many studies (albeit not all) fail to do this. However, Fitzpatrick and Shaffer *do* have a plausible mechanism for selection on BTS in perennial pools (i.e., their ability to retain aquatic characteristics), so their study satisfies this desideratum. (In my experience, provision of the causes is the rule in studies that combine ecology with population genetics rather than the

¹⁴ Fitzpatrick and Shaffer elaborate, “The cues used by amphibians to emerge from their underground retreats in a Mediterranean climate are poorly understood. It is probably determined in part by physiological clocks and in part by how individuals experience the weather and other seasonal stimuli in their subterranean terrestrial habitat, rather than by the pond in which they will breed. Nonrandom fertilization seems unlikely to be affected much by the pond environment, although spermatophores may spend several minutes in the open water prior to internal fertilization.... Other factors are more likely to have strong environment dependence. For example, visual or olfactory mate choice systems may be disrupted in the turbid, eutrophic water of artificial ponds, potentially explaining why there is a deficit of *DLX3* heterozygotes only in the less turbid vernal pools. Alternatively, components of the physical or biotic environment may cause stronger viability selection on embryos and young larvae in vernal pools. The habitat-dependent heterozygote excess at *HOXD8* could arise because cattle ponds may present immunological challenges that would be unusual in cleaner vernal pools, leading to balancing selection or heterosis in gene regions involved in pathogen response” (Fitzpatrick and Shaffer 2004, p. 1290). Although one referee of this paper suggested that Fitzpatrick and Shaffer’s explanation amounts to “hand waving,” I think it is an example of how knowledge of organisms in their habitats can help to overcome some of the problems with HWE analysis. Of course, such explanations are defeasible, as Fitzpatrick and Shaffer readily acknowledge.

exception—indeed, that seems to be a large part of the point of such studies—but resolution of this disagreement is beyond the scope of this paper.) Pigliucci and Kaplan further suggest that substantiating selection requires a “detective” rather than a “statistician.” However, those who integrate population genetics with ecology can be both. It is not an either-or proposition.

As Fitzpatrick and Shaffer (2007) describe, there are also some broader issues raised by the study of the CTS. First, there is the perennial question, “what is a species?” The answer has considerable practical import because, under the U.S. Endangered Species Act, only *species* (and not, e.g., sub-species) are explicitly listed for preservation. The CTS and BTS produce viable hybrids, yet they were distinct lineages for ca. 5 million years and have distinctive phenotypes and genetic characters. Should they be considered two species or one? If left alone, would the hybrids yield a new species? Or a return to an old?

Other questions raised by the study of the CTS and the BTS include: Should we try to conserve *both* CTS and BTS? Is hybridization an extinction process for the CTS? Or should we conserve hybrids? Should we recommend converting perennial ponds to ephemeral ponds, which might help preserve the CTS, as a management strategy? Tiger salamanders can have substantial effects on the distribution and abundance of aquatic arthropods, frogs, and other salamanders; how does hybridization of the tiger salamanders affect them?

By revealing the rates, patterns, and mechanisms of hybridization, population genetics combined with ecology has a central role to play in answering each of the above questions (contra Dupré’s 1993 contention that population genetics has no practical benefits).¹⁵ However, someone might be willing to grant these points, and yet not see how population genetics has changed through its contact with ecology. After all, the population genetics used in Fitzpatrick and Shaffer (2004) seems close to the very traditional and narrow characterization of population genetics mentioned above: “Models that have their roots in Hardy–Weinberg equilibrium.”¹⁶ So, let us turn to another study from the Shaffer Lab Group that fits the broader characterization of population genetics that I gave above: “Models that track or infer frequency changes in genotypes

¹⁵ Note that my claim is *not* that the Shaffer Lab is the only, or even the first, to perform such studies. For example, the Collins Lab at ASU performed similar studies of a species of salamander native to Arizona, raising many similar ethical and policy issues (Jones et al. 1995; Maienschein et al. 1998; Storfer et al. 2004). Rather, my claim is that the Shaffer Lab studies are illustrative of many such excellent studies.

¹⁶ Although Fitzpatrick and Shaffer certainly go beyond a one-locus, two-allele model!.

and phenotypes over time, and the way that various evolutionary mechanisms affect those changes.”

“Landscape Genetics and Least-Cost Path Analysis Reveal Unexpected Dispersal Routes in the California Tiger Salamander”

Wang et al. (2009) characterize their study as a contribution to the burgeoning field of landscape genetics, mentioned briefly above. One goal of landscape genetics is to understand how landscapes affect genetic variation in natural populations; Wang et al., this time focusing solely on the CTS, elaborate on this relationship. In particular, as Fitzpatrick and Shaffer (2007) show in an earlier ecological/landscape genetics analysis, habitat affects gene flow, but can this relationship be quantified? In this study, noting that it is almost impossible to directly study the migration of organisms such as the CTS (which spends much of its adult life in underground burrows), they use an alternative approach, one which makes use of the “integration of GIS-based tools with population genetic analyses” (Wang et al. 2009). The study area consisted of the habitats surrounding a relatively isolated and intact set of sixteen¹⁷ natural vernal pools in Fort Ord Natural Reserve. They used two main types of analysis: a genetic assignment method using 13 microsatellite loci, implemented in BayesAss+, and a GIS least-cost path analysis. The former is a Bayesian multilocus genotyping method for estimating rates of recent migration among populations.¹⁸ The latter seeks to identify dispersal corridors and determine the cost of movement through the three identified habitat types (grassland, chaparral, and oak woodland). They constructed a detailed habitat map based upon satellite imagery and field surveys, scoring each cell with a value corresponding to either vernal pool or one of the three habitat types. They then performed 24,843 least-cost path analyses, run on different possible combinations of costs, in order to find combinations of cost values that would result in least-cost path distances predicted by the gene flow estimates (assuming higher rates of gene flow indicated relatively less costly dispersal).

¹⁷ Their BAPS software, looking for significant allele frequency differences, identified 15 different populations.

¹⁸ As Wilson and Rannala explain, “The method requires fewer assumptions than estimators of long-term gene flow and can be legitimately applied to nonstationary populations that are far from genetic equilibrium. Moreover, the newly proposed method relaxes a key assumption of previous nonequilibrium methods for assigning individuals to populations and identifying migrants—namely that genotypes are in Hardy–Weinberg equilibrium within populations. We allow arbitrary genotype frequency distributions within populations by incorporating a separate inbreeding coefficient for each population. The joint probability distribution of inbreeding coefficients is estimated from the data” (2003, p. 1178).

Based on Wang et al.'s BayesAss+ analysis, four ponds showed significant rates of dispersal, and these rates were also quite high; 10.5–19 % of the target populations could be explained by gene flow from the source. Based on their least-cost path analysis, Wang et al. conclude that migration through chaparral is the least costly to the CTS; movement through grassland is approximately twice as costly as through chaparral, and movement through oak woodland is roughly five times as costly as through chaparral. This was a surprising result, since the CTS is normally associated with a grassland habitat; Wang et al. speculate that whereas the CTS may prefer to reside in grassland, it may prefer to move through chaparral. Wang et al. state that “Landscape genetics is playing *an increasingly important role in population genetics* by providing a framework for quantitatively modelling the effects of landscapes on gene flow, population substructure, and genetic variation,” (2009, p. 1373; emphasis added) and indeed, I think it is fair to say that their analysis of the CTS is a beautiful demonstration of how this is possible. And again, the conservation significance is clear.

The two studies of the CTS that I have described here illustrate some of the ways in which ecology and population genetics can intersect. In the first, ecological knowledge informs our population-genetics-based conclusions, with the population genetics models being used in a fairly standard way. The second study extends the ecological genetics analysis of Fitzpatrick and Shaffer (2007), which showed how correlational analyses can shed light on the ways that habitat affects population genetics processes such as gene flow and selection, by showing how such effects can be quantified, setting the stage for further integration between population genetics and ecology.

Conclusions

I conclude with some reflections about theory in general and about population genetics in particular. With respect to theory in general, I think two major insights can be drawn from this examination of population genetics and ecology. The first is that, while some of this work can be described as almost purely theoretical/mathematical, and while it is easy to play up the split between theoreticians and empirically-driven scientists, I think much of the work discussed here does not fit these neat categories, with empirical findings driving the need for better models (e.g., density dependence), and with new mathematical tools allowing for better analyses in the field (e.g., GIS least-cost path analysis and BayesAss+ analysis; see Griesemer [2012, this issue] for a more extended discussion of the interplay between theory and empirical practice). Second, although a number of philosophers have sought to analyze the nature

of theory change (e.g., Kuhn 1970; Lakatos 1978; Hull 1988; Darden 1991), they have generally seen theory change as a linear process (Darden may be the exception here). Yet the intersections between ecology and population genetics highlighted here are hardly linear. Rather, they are multi-stranded and overlapping. Moreover, there are parts of ecology and population genetics that do *not* overlap with each other, and there are innumerable models, each representing a partial approach (see Longino 2012, this issue) to representing evolutionary and ecological processes. So, a neat and tidy picture of theory change will not work for these domains. We need a picture that shows theories changing in multiple directions, driven by a variety of empirical and theoretical requirements, separately and in tandem.

With respect to population genetics in particular, I hoped to have shown the following.

Population genetics is more than an abstract set of tools found in textbooks; it can and has been applied to real organisms and their traits, and real-world situations and problems.

Population genetics has undergone continuous and significant changes since the 1950s, in part by integrating with other fields such as ecology, with the boundaries between fields becoming more blurred over time (see Lynch 2007 and Futuyma 2010 for discussion of other types of changes). Furthermore, those changes have been in many directions: niche construction, landscape genetics, etc. (again, this is not to deny that some population genetics work continues to have little contact with ecology and vice versa).

Thus, if we are to discuss the role of population genetics in evolutionary theory, we need to use a *contemporary* characterization of it. If we are going to discuss what a theory doesn't do (e.g., incorporate development), we should not forget what it can do (e.g., form productive intersections with ecology). And if we are to discuss the possibility of or the need for Extended Synthesis to include development, we need to recognize that *many* syntheses have already occurred—so, with which version should we synthesize? Population genetics may not be required for all evolutionary explanations (contra Lynch 2007, although I have not sought to argue that point here), and it may not incorporate all the causal factors of evolution, but it is a powerful tool that continues to be used and modified.

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