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Populations crossing habitat boundaries in the face of environmental change

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General Introduction

Catalina Chaparro Pedraza

1.1 – FOUNDATIONS OF AN EXPLANATORY AND PREDICTIVE SCIENCE

"Theoretical population biology is the science of the possible; only direct observation can yield a knowledge of the actual." - Lewontin (1968)

In any population, the number of individuals changes over time in response to biotic and abiotic factors i.e. resource availability, predation, disease, competition, climate. How those factors affect the rate of change of population abundance is the main focus of population ecology. Relevant empirical observations, theories, models and hypotheses exist for this problem. Empirical observations provide us with information about abundance or density of a specific population in a particular time; but unless this information is integrated in a larger body of knowledge it may be of little use to ecologists who did not conduct the empirical study. Hence, ideally, evidence documented in individual empirical studies is integrated into theory (Michael 2002). The purpose of theories is to explain and to predict phenomena (Kerlinger 1966). Specifically in population ecology, theories aim to explain by identifying the possible factors and the relationships among them that cause the population dynamics and to predict the possible consequences of a certain set of factors for the population dynamics (Lewontin 1968). The antecedent-consequent (cause-and-effect) nature of the explanatory and predictive purposes of a theory entails a mechanistic explanation.

"By calling the explanations mechanistic, we are highlighting the fact that they treat the systems as producing a certain behavior in a manner analogous to that of machines developed through human technology. A machine is a composite of interrelated parts, each performing its own functions, that are combined in such a way that each contributes to producing a behavior of the system. A mechanistic explanation identifies these parts and their organization, showing how the behavior of the machine is a consequence of the parts and their organization." - Bechtel and Richardson (1993)

Mechanisms consist of entities and activities organized such that they produce the phenomenon of study (Craver 2007). Entities are the components of the mechanism and activities are what they do. Components of mechanisms producing ecological phenomena come from various levels of biological hierarchy that extend from molecules and cells to organisms and ecosystems and include inanimate objects or processes (Pâslaru 2014). Since properly organized activities of components are responsible for causing the phenomenon, mechanistic explanations in population ecology must describe the relevant behaviors of individuals and inanimate components (i.e. resources, abiotic conditions), integrating information from various levels of organization.

"How could our seemingly old-fashioned subjects (i.e., ecology and evolutionary biology) achieve new intellectual rigor and originality compared to molecular biology? What can we learn from molecular biology on how to advance our own science? We agreed that the basic problem was that ecology and evolutionary biology were mostly unrooted. They needed foundations from which explanations can be developed bottom-up. Theory has to work from lower to higher levels of biological organization. Either alone will not do. Population biology was the discipline we thought could serve as base to reinvigorate the theory of ecology and evolutionary biology." - Wilson (2009)

In the first theoretical models in population ecology, such as Lotka-Volterra models, the relevant behaviors of individuals included reproducing, dying, competing, feeding, predating; posteriorly, behaviors such as moving and dispersing were introduced in spatial population ecology studies. More recently, other behaviors regarding individual development, such as growing, maturing, and developing, have been added to population ecological theory. Such behaviors of individuals and inanimate components establish relationships that are causal in ecological mechanisms and thus exploitable for manipulation and control (Woodward 2005). Therefore, one can formulate predictions of what are the consequences of specific values regarding the behavior of individuals (i.e. feeding rate, growth rate, mortality rate) and inanimate components (i.e. temperature variability, resource availability) for the population dynamics. Yet, formulation of accurate predictions requires accurate description of mechanisms (Páslaru 2014).

"How fast is ecology moving forward? If we quantify progress by how predictive ecology is, then progress has been slow and insufficient to solve many problems related to the loss of biodiversity, global changes in climate and land use and the potential collapse of ecosystem services. Ecology will not be able to solve these problems alone, but without improving its predictiveness, there might be no solutions at all." - Grimm and Railsback (2012)

Predictions play an important role in biodiversity management policy, as they alert about potential risks, provide a means to attribute biological changes to a particular factor and support the development of strategies to reduce negative impacts (Bellard et al. 2012). Predictiveness in ecology is therefore necessary to address the multiple impacts of environmental change rapidly occurring (Grimm and Railsback 2012; Karl and Trenberth 2003). However, accurate ecological predictions have proved difficult to formulate (Dawson et al. 2011; Grimm and Railsback 2012).

To date, assessments of impacts on populations due to environmental change typically rely on descriptions of processes coming from aggregated population data

(Chevin et al. 2010; Dawson et al. 2011). The limited ability of those approaches to accurately predict is therefore not surprising, and can be attributed to the focus of traditional ecological theory on patterns at a single level of organisation (Clark et al. 2011; Grimm and Railsback 2012). As I argued above, accurate ecological predictions arise only from accurate descriptions of ecological mechanisms that have components coming from various levels of biological organisation.

Ecological systems are complex systems whose properties at higher levels emerge from interactions among components at lower levels (Levin 1998). Therefore, a pattern observed at the population level cannot be mechanistically explained by describing only the population properties rather than the behavior of individuals and their interactions with the environment and other individuals. Elucidating interactions between components and processes acting at different biological levels of organisation may be challenging but is necessary to attain mechanistic understanding of ecological systems. In a theoretical foundation that serves as a framework of an explanatory and predictive ecological science, mechanistic understanding of ecological systems is certainly required. This thesis aims to contribute to this theoretical foundation by providing a mechanistic understanding of the effects of changing environmental conditions on populations. In the following sections of this introduction, I will discuss what components are essential in this theoretical foundation.

1.2 – CHANGING ENVIRONMENT

As the human population continues to increase and its activities to expand, global climate change, biodiversity loss, land cover transformation and pollution intensify. Almost all ecosystems on Earth are facing the impacts of environmental change at all biological scales through a wide variety of stressors. Although most biological effects have been recorded at a single scale, there is evidence that changes at individual and population level are intimately linked (Parmesan 2006). Given the nature of ecological systems organisation, in which properties at higher levels (i.e. population, species) emerge from interactions among components at lower levels (i.e. individuals), such joint responses should be the rule. However, the mechanisms causing these joint responses to environmental change are rarely identified because most efforts have focused on these responses of population or even species in an aggregated way (but see Ozgul et al. (2010); Thompson and Ollason (2001)). Nonetheless, populations do not respond to the environment, only individuals do (Clark et al. 2011) and these responses may differ among individuals.

Organisms differ in their requirements and demographic rates in different life stages. Those differences may make individuals more or less susceptible to distinct stressors during different life stages. Consequently, the effects of a particular stressor

on the population depend on the life stage that is susceptible to it. For instance, a particular stressor reducing the feeding rate of juveniles does not directly affect population growth because juveniles do not reproduce; in contrast, reduced feeding rate of adults decreases individual fecundity and thus population growth.

Accounting for the multiple individual responses to a particular individual stressor may have counterintuitive consequences for populations. For example, competition for food resources between juveniles and adults can result in an increase in the total population biomass when mortality increases (i.e. biomass overcompensation (de Roos et al. 2007; Persson and de Roos 2013)). Therefore, assessing the consequences of environmental change for populations requires a consideration of its impacts on individual life history.

Characterizing responses to environmental change for communities and ecosystems may be even more challenging. Biotic interactions are a fundamental organizing feature of ecological communities and therefore need to be integrated in a theoretical framework that enables predicting how environmental change impacts community composition and stability. In fact, recent work has highlighted that considering biotic interactions improves our ability to predict biological responses to environmental change (Gilman et al. 2010; Mellard et al. 2015).

It is increasingly acknowledged that environmental change does not only have direct effects on individuals but it influences interactions between them. For instance, stress avoidance can alter activity patterns (Tuomainen and Candolin 2011) affecting encounter rates between competitors, between prey and predator or between parasite and host. Although progress is being made to integrate biotic interactions into assessments of biological consequences of environmental change (Thuiller et al. 2013), most studies have assumed interactions between species to be constant. However, hypothesized interactions between species do not operate at the species level but at the individual level (Clark et al. 2011). In other words, species do not interact, individuals do.

Interactions between individuals do not remain constant throughout life history. For most animal species the outcome of encounters with competitors, potential prey and predators depends on the life stage of the interacting organisms. For instance, in aquatic ecosystems the majority of predator species do not have a predatory diet as small juveniles. While adult predators reach large body sizes and prey on smaller fish species, the body size of a predator species at birth is often similar to that of their future prey (de Roos and Persson 2013). Hence, these small juvenile predators necessarily feed upon other types of food that might be the same as the food types of their future prey; therefore individuals of a predator and prey species may be engaged in a competitive or a predatory interaction depending on the life stage of the predator individual interacting. These ecological transitions between different life

stages involving a shift in food resource or habitat use are widespread across various taxa of the animal kingdom (Werner 1988). Those shifts result in complex interactions in natural communities because individuals in different life stages face different competitors and predators. The interplay between individual life history and biotic interactions is causal in ecological mechanisms shaping population abundance and community composition (de Roos and Persson 2002, 2013; Persson and de Roos 2013). Therefore, this interplay cannot be overlooked if we aim to accurately predict effects of environmental change on population abundance and community composition.

1.3 – ECO-EVOLUTIONARY DYNAMICS

"At every moment natural selection is operating to change the genetic composition of populations in response to the momentary environment, but as that composition changes it forces a concomitant change in the environment itself. Thus organisms and environments are both causes and effects in a coevolutionary process." - Lewontin (2001)

One of Darwin's greatest insights was to recognize that populations have the potential to grow exponentially, but confronted with the limited resources provided by the environment, individuals that compete the best would have the best chance to survive and procreate (Darwin 1859). Therefore, the idea that ecological processes influence evolutionary processes by setting a selective environment for evolution has been deep-seated in evolutionary theory since its origin. Instead, the opposite idea that evolutionary processes influence ecological processes had been disregarded based on the traditional belief that evolutionary change does not proceed sufficiently fast to be observable on ecological timescales. However, there is growing empirical evidence that evolutionary and ecological processes can occur in commensurate timescales and that evolution can have significant ecological effects (Pelletier et al. 2009; Schoener 2011). In Darwin's finches, for instance, evolutionary contributions to population growth were estimated to exceed ecological contributions (Hairston et al. 2005).

The realization that evolutionary dynamics can affect ecological dynamics has opened the door to the possibility that they interact in a feedback loop. If in addition to the long supported idea that ecology can affect evolution, evolution can affect ecology, then the transformed ecology may influence evolution, and so on, back and forth (Schoener 2011). The bidirectional feedback therefore requires 1) that organisms strongly impact the environment in which they reside and, 2) that the altered environment differentially affects the fitness of phenotypically diverse individuals (Post and Palkovacs 2009). In this loop, one pathway corresponds to the effect exerted by phenotypic changes on the population density and composition, and the second pathway

corresponds to the effect that population density and composition has by differentially favoring certain phenotypes in the population.

The interaction between ecological and evolutionary processes has effects not only at the population but also at the community level. The fitness of an individual is the result of its interactions with competitors, resources and natural enemies. The strength and outcome of ecological interactions are influenced by the phenotypic traits of the interacting individuals. Hence, natural selection can cause changes in ecological phenotypic traits such as habitat or resource use that can alter ecological interactions, and these in turn have an effect on individual fitness and thus are subjected to natural selection.

There are an increasing number of documented examples of this effect of community composition on the evolution of life history and ecological traits and the feedback effect of this evolution on community composition. In a consumer-resource interaction between rotifers and green algae, population genotype composition of the resource varies in response to variations in the abundance of the consumer in the system. A resource variant carrying costly defense against predation increased in frequency as the consumer density increased, while the frequency of an undefended resource variant with higher intraspecific competitive ability increased as the consumer density decreased in response to the increase in the defended variant (Yoshida et al. 2003). Likewise, predator density affects individual life history and density of populations of guppies and these changes in turn have an effect on resource availability and subsequently on diet preference (Reznick et al. 2001, 1996). Similarly, eco-evolutionary feedbacks have been reported in communities in which species coevolve between intra- and interspecific competitive abilities, resulting in oscillations of species abundance in the community (Lankau and Strauss 2007). Furthermore, the impact of eco-evolutionary feedbacks goes beyond the community level by altering ecosystem processes such as nutrient cycling and productivity (Pelletier et al. 2009). Therefore, considering the interaction between ecological and evolutionary processes is fundamental to studying how population abundance, community composition and ecosystem functioning are shaped.

Changing environmental conditions do not only affect population densities but also selective pressures. Rapid changes in phenotypic traits of wild populations have been documented as a result of changes in selective pressures caused by the novel conditions imposed by environmental change (Allendorf and Hard 2009; Olsen et al. 2004; Palkovacs et al. 2012; Singer et al. 1993). Most research addressing the effects of environmental change has focused on its ecological consequences while its evolutionary consequences have received less attention (Urban et al. 2012). Recent synthetic efforts have demonstrated the emergence of unexpected phenomena when both ecological and evolutionary processes are considered in concert and have highlighted the need

of a strong eco-evolutionary theoretical foundation to generate accurate predictions regarding the effects of environmental change on population abundance and community composition (Bolchoun et al. 2017; Norberg et al. 2012; Palkovacs et al. 2012; Urban et al. 2012).

1.4 – ONTOGENETIC SHIFTS IN HABITAT USE

Most animal species undergo major ecological transitions between different life stages that involve a shift in food resource and possibly habitat use (Werner 1988). Although best-known examples of species with an ontogenetic habitat shift correspond to species undergoing metamorphosis, such as amphibians, holometabolous insects or marine invertebrates, it is also common in non-metamorphic species including fish (Hampton 2000; Krause et al. 1998; Mittelbach and Osenberg 1993; Sogard 1997) and reptiles (Ferguson and Fox 1984; Keren-Rotem et al. 2006). For instance, various salmonid species breed in freshwater and subsequently migrate to the ocean. Sticklebacks begin their life cycle in the benthic environment and afterwards become pelagic. Similarly, in some species of coral reef fish only old individuals use the coral reef ecosystem while young ones use mangroves as nursery habitats.

One of the most remarkable types of ontogenetic habitat shift is anadromy, a life-history behavior in which individuals use oceans and freshwater habitats for feeding and reproduction, respectively, during different life stages. The anadromous life cycle begins in freshwater (the breeding habitat), where early development takes place. Afterward individuals migrate to the ocean (the non-breeding habitat), where they grow larger, mature and subsequently return to freshwater for spawning.

Anadromous fish migrations have fascinated humans since ancient time. In the oral tradition of native American tribes, there are stories that evidence the cultural importance of salmon migration as it fed large numbers of people on a seasonal basis (Hymes 1985). Nowadays, anadromous fish species including salmon, sturgeons, and shads are of particular concern because of their economic and cultural importance: although these species comprise overall less than 1% of the world fish fauna, their share in global fisheries trade currently exceeds 17% and continues to increase (Food and of the United Nations. Fisheries Department 2016). However, major declines in anadromous wild populations have been documented in the last decades (Limburg and Waldman 2009).

Multiple threats have contributed to the decline of anadromous populations, including infrastructure building in freshwater streams, overfishing, pollution and climate change (Limburg and Waldman 2009). Those threats do not have equal impact on the freshwater and the marine habitat and as a consequence their effects differ among individuals in different life stages. For instance, reproducing individuals are

more vulnerable to infrastructure building in freshwater streams as it obstructs their migratory routes to the spawning grounds, while it does not have a direct effect on young individuals. Because individuals in different life stages contribute in different ways to the population dynamics (i.e. juveniles do not reproduce and thus do not contribute to population growth, whereas instead, adults do), the impact of a particular stressor on the population depends on the life stage that is susceptible to it. Effects of threats on an anadromous population therefore are the result of multiple responses of individuals in different life stages that make up the population. Hence, accurately assessing impacts of threats on anadromous populations certainly requires a consideration of the different responses throughout individual life history.

Since environmental change impacts frequently differ across habitats, the last statement in the previous paragraph holds more generally and can be extended to other life cycles involving an ontogenetic habitat shift. Given that in species with an ontogenetic habitat shift individuals in different stages use different habitats, the impact of environmental change on the population varies depending on its effects on either habitat and thus on either life stage. Therefore, an explicit description of the individual life history is required to accurately assess the consequences of environmental change for populations with an ontogenetic habitat shift. In addition I argued in a previous section for a greater emphasis on the interplay between individual life history and biotic interactions in a framework to study the effects of environmental change on population abundance and community composition. This interplay is especially relevant for populations with an ontogenetic habitat shift because the community composition differs in the two habitats and therefore the habitat shift implies as well a shift in interactions with food resources, competitors and predators.

In summary, I have argued that individual life history, ecological interactions, and eco-evolutionary dynamics are essential components of a theoretical foundation that serves as a framework of an explanatory and predictive ecological science.

In that context, this thesis aims to reveal the ecological and eco-evolutionary consequences of changing environmental conditions on the dynamics of populations with an ontogenetic habitat shift. It focuses in particular on revealing and understanding the mechanisms by which populations with an ontogenetic habitat shift respond to changing ecological conditions and does so by considering both the ecological as well as the eco-evolutionary consequences of the interplay between individual life history and resource-consumer interactions.

1.5 – RESPONSES TO A CHANGING ENVIRONMENT WHEN LIFE HISTORY INVOLVES A HABITAT SHIFT

This thesis studies the ecological (chapters 2 and 3) and eco-evolutionary (chapters 4, 5 and 6) consequences of changing environmental conditions on populations with an ontogenetic habitat shift. To study the ecological consequences, I use the framework of Physiological Structured Population Models (PSPM) that allows for the explicit description of the individual life history, and ecological dynamics at higher levels (i.e. population and community) then emerge from the interaction between individuals and their environment. An individual bioenergetics approach is used to link the food resource available in the environment to individual feeding, body growth and fecundity. To study the eco-evolutionary consequences, I also use the adaptive dynamics and population genetics approaches that allow analyzing phenotypic evolution based on the ecological dynamics predicted by the PSPM approach.

Since the effect of changing environmental conditions on a population with a habitat shift depends on its effects on the different life stages that are susceptible to it, chapter 2 and 3 study the consequences for the entire population of changes in ecological conditions directly affecting only individuals in a particular life stage. Specifically, I study how increased energetic costs of the breeding travel and reduced survival and food availability in the non-breeding habitat affect an anadromous population. These three unfavorable ecological conditions affect directly only older individuals in the population. In both chapters, I use a population model in which continuous dynamics describe the individual resource consumption, body growth, reserves dynamics and survival and a discrete map describes the pulse-wise reproduction (Persson et al. 1998). In chapter 2, I investigate the independent effect of these unfavorable conditions on the entire population and their indirect effect on other life stages via changes in population processes. This chapter identifies some mechanisms causing joint responses in life history traits and population dynamics as a consequence of changing environmental conditions. In chapter 3, I investigate the effects of these unfavorable conditions affecting the population in a cumulative way. In this chapter, two unfavorable conditions with independent negative effects show a highly non-linear type of interaction leading to a counterintuitive, beneficial effect on population persistence as a consequence of the specifics of the anadromous individual life history.

The two habitats used throughout the individual's life differ in a variety of conditions including food abundance and mortality risk. As a result, individuals experience multiple changes during the habitat shift that influence their survival, growth and fecundity. Therefore, the timing of the habitat shift is fundamental in determining individual fitness and thus subjected to selection. In chapters 4, 5, and 6 I investigate the eco-evolutionary consequences of changing environmental conditions on a population

in which the timing of the habitat shift evolves. To do so, I formulate a population model in which all life history processes, including individual food consumption, body growth, survival and fecundity, follow continuous-time dynamics. Because small individuals are usually more vulnerable to predation than large ones (Hampton 2000; Krause et al. 1998; Sogard 1997), in chapter 4, I investigate the relative role that size-dependent and size-independent mortality have on the evolution of the timing of the habitat shift. I found that through indirect effects mediated by changes in population structure, the nature of the mortality source (size-dependent vs. size-independent) influences the evolution of this life history trait in previously unexpected ways. In chapter 5, I examine the role of mortality risk and food resource productivity on the interaction between ecological and evolutionary dynamics. This chapter shows that eco-evolutionary feedbacks may drive phenotypic changes in the timing of the habitat shift and that these changes impact community dynamics. In chapter 6, I study how changes in mortality risk influence the eco-evolutionary dynamics of the timing of a habitat shift and describe a new mechanism whereby changes of abiotic conditions cause delayed regime shifts in nature.

In chapter 7, I summarize the results of the thesis and discuss how they contribute to understand the effects of a changing environment on populations with an ontogenetic habitat shift. I will then conclude by suggesting directions for future research.

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