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Populations Crossing Habitat Boundaries in the Face of Environmental Change
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Summary

Populations crossing habitat boundaries in the face of environmental change

Almost all ecosystems on Earth are facing the impacts of rapid environmental change. As the human population continues to increase and its activities expand, biodiversity loss and global changes in climate and land cover intensify. Environmental change is occurring at unprecedented rates (Steffen et al. 2006) and is causing shifts in species distributions, abundances, phenology, physiology and morphology (Bellard et al. 2012; Dawson et al. 2011; Ozgul et al. 2010). Accurate predictions are needed to supply managers and stakeholders with potential responses of biological systems to environmental change in order to facilitate decision-making in conservation management. However, we have largely failed to generate accurate predictions regarding environmental change responses (Dawson et al. 2011; Gilman et al. 2010; Grimm and Railsback 2012).

In chapter 1 of this thesis, I argue that the failure to generate accurate predictions stems from the fact that predictive studies of environmental change are not based on a strong theoretical foundation in which population and community dynamics emerge from interactions between individuals and their responses to the environment. In fact, assessments of environmental change impacts on populations typically rely on descriptions of processes coming from aggregated population data (Chevin et al. 2010; Dawson et al. 2011). Nonetheless, populations do not respond to the environment, individuals do (Clark et al. 2011), therefore, the limited ability to accurately predict is not surprising. Impacts of environmental change on populations and communities are the consequence of the multiple responses of individuals that make up these populations and communities. Accurately predicting population and community consequences of environmental change therefore requires an explicit description of the multiple individual responses.

Environmental change is not uniform; in fact, its impact differs across habitats. Organisms living in different habitats therefore experience different effects of a changing environment. Many animal species change their habitat throughout their lives (Werner 1988). Species with an ontogenetic habitat shift use different habitats in different life stages. One of the most remarkable types of ontogenetic habitat shift is anadromy, of which salmon life cycle is one of the best-known examples. The anadromous life cycle begins in freshwater, individuals subsequently migrate to the ocean, where they grow larger and eventually become mature, after which they migrate back to freshwater for reproduction. Therefore, in a population with an ontogenetic habitat shift the impact of environmental change varies depending on its effects on either habitat and thus on either life stage. An explicit description of the individual life history is required to accurately assess the consequences of environmental change on populations with an ontogenetic habitat shift. By considering the effects of changing environmental conditions on individual life histories, this thesis investigates the ecological (chapters 2 and 3) and eco-evolutionary (chapters 4, 5 and 6) consequences of those changing conditions on populations with an ontogenetic habitat shift.

There is growing evidence that effects of a changing environment on individuals and populations are intimately linked (Parmesan 2006). However, the mechanisms causing these joint responses remain largely unidentified. Chapter 2 contributes to filling this gap by identifying the mechanisms causing joint responses in life history traits and population dynamics of anadromous populations exposed to deteriorating environmental conditions. Specifically, I study what the effects of increased energetic costs of the breeding migration and reduced survival and food availability in the ocean are on an anadromous population. These threats directly affect only individuals in late life stages (oceanic life stage), however its indirect effects include apparently positive effects such as high body growth rate in other life stages. Low survival and low food abundance in the habitat used by older individuals, as well as high cost of the breeding migration, negatively impact the population birth rate. As a consequence of low population birth rate, individual density in the breeding habitat is low and thus decreased competition for food resources enables a higher body growth rate. This mechanism therefore explains the relation between negative impacts on individuals of late life stages and increased body growth rate in other life stages. This mechanism reveals that increased growth rate of individuals in the freshwater habitat may be a signal of population decline and negative impacts affecting individuals in the oceanic life stage.

Current environmental changes increase the diversity and intensity of stressors affecting ecological communities simultaneously, however the cumulative and interactive effects of various stressors in combination are poorly studied (Crain et al. 2008). While in chapter 2, I investigate the independent effects of increased energetic costs of the breeding migration and reduced survival and food availability in the ocean; in chapter 3, I investigate the cumulative effects of these deteriorating conditions on a population. Chapter 3 shows that multiple stressors may interact in a highly non-linear manner and thereby, counterintuitively, mitigate each other's negative effect. On their own, both increased cost of the breeding migration and low marine food levels negatively affect anadromous fish populations, as shown in chapter 2. But, unexpectedly, low marine food levels favor, as opposed to threaten, the ecological success of anadromous populations negatively affected by increased cost of the breeding migration. This counterintuitive effect is due to the fact that individuals switching to higher food levels in the ocean reach larger sizes with concomitant larger migration costs but have lower energy densities. The individual energetic budget has a key role in the mechanism causing the counterintuitive effect. Stressors mainly interact in a non–linear manner (Crain et al. 2008), hence predicting the consequences of multiple stressors affecting a population in a cumulative way requires gaining further insight into the mechanisms causing these non-linear effects. Chapter 3 demonstrates how such consequences can be investigated by integrating individual energetics and life history into population models.

In populations with an ontogenetic habitat shift, the timing of this shift has multiple effects on individual and population processes. Since the two habitats used by individuals in different life stages differ in a variety of conditions including food abundance and mortality risk, 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. Effects of environmental change on food abundance and mortality risk may differ across the habitats used in different life stages, hence changing environmental conditions may shift the optimal timing of the habitat shift and thus trigger phenotypic changes on this life history trait. The timing of an ontogenetic habitat shift influences population processes by determining the outflow and inflow of individuals in the two habitats and thus the density of individuals in each habitat that. High density of individuals in either habitat imposes a high foraging pressure that causes the depletion of food resource in this habitat. Conversely, in a habitat with low density of individuals food is abundant. Food availability, in turn, influences the optimal timing of an ontogenetic habitat shift by altering individual survival, growth and fecundity.

Consequently, the feedback between individual and population processes is fundamental to understand how a changing environment produces evolutionary changes in the timing of an ontogenetic habitat shift, which in turn causes ecological changes.

Traditionally, the evolution of the timing of an ontogenetic habitat shift has been studied in a context of individual optimization of fitness that ignores ecological interactions between individuals. However, the fitness of an individual is the result of its interactions with competitors, resources and natural enemies. These ecological interactions do not remain constant throughout individuals' lives. For instance, small individuals are usually more vulnerable to predation than large ones (size-dependent mortality). Chapter 4 demonstrates that size-dependent and size-independent mortality differ in their effects on the structure of a population with an ontogenetic habitat shift that causes changes in the strength of competition. As a consequence of these effects, the nature of the mortality source (size-dependent vs. size-independent) influences the evolution the timing of an ontogenetic habitat shift in the opposite direction of selection than was expected in a context of individual optimization of fitness. Environmental change frequently alters population abundance (Ehrlén and Morris 2015) and structure (Allendorf and Hard 2009), which, in turn, affect interactions with competitors in the population. Chapter 4 demonstrates that those interactions can shape the evolution of life history traits and, therefore they cannot be overlooked when investigating the eco-evolutionary consequences of a changing environment.

As a consequence of a life cycle with an ontogenetic habitat shift, the different habitats hosting different life stages are indirectly connected through the flux of individuals between them. It is increasingly recognized that such connections can have strong impacts on the structure and dynamics of the local communities (Doughty et al. 2016; Polis et al. 2004; Sánchez-Hernández et al. 2018). Although those ecological impacts are well known, their interactions with evolutionary dynamics are not yet studied. Chapter 5 shows that the interaction between ecological and evolutionary dynamics drive changes in the timing of the habitat shift and that this evolutionary process can, in turn, cause gradual and abrupt ecological changes in the communities that host the different life stages.

We have witnessed abrupt and dramatic transitions in the composition and functioning of diverse ecosystems, including lakes, coral reefs, deserts, woodlands and oceans. These so-called regime shifts are attributed to the existence of alternative ecosystem stable states for the same set of conditions. Traditionally, ecologist have considered the occurrence of these abrupt regime shifts to a dramatically contrasting ecosystem state when changes in abiotic conditions occur beyond a threshold (tipping point)(Scheffer et al. 2001). In contrast to traditional ecological theory, chapter 6 demonstrates that changes in these conditions may not occur beyond a threshold and therefore do not immediately cause an abrupt transition to a contrasting state, but can nonetheless result one with a substantial time delay due the evolutionary process that is triggered by the change in conditions. This suggests that regime shifts in ecosystems observed in the present may be the consequence of perturbations that occur in the distant past but we would fail to attribute a regime shift to its perturbation if we ignore the evolutionary process initiated by the perturbation. Chapter 6 contributes to the body of theory on ecosystems resilience by presenting a new mechanism whereby changes in environmental conditions cause delayed regime shifts in nature.

The results presented in this thesis contribute to an understanding of the mechanisms whereby changes in populations with an ontogenetic habitat shift occur as a result of a changing environment. Characterizing these mechanisms required the consideration of the multiple responses of individuals that make up the population, specially, the different individual responses throughout life history. Individuals depend on their environment and the environment is the product of the organisms that inhabit it. Therefore, if we are to predict ecological consequences of environmental change and thus to adopt conservation measures accordingly, mechanistic understanding of how individuals interact between them and with their environment is certainly required.

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