Ecological Modeling of Adaptive Evolutionary Responses to Rapid Climate Change

---

Daniel Romero Mujalli

Univ.-Diss.

zur Erlangung des akademischen Grades
"doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin Evolutionsbiologie

eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
Institut für Biologie und Biochemie
der Universität Potsdam

Ort und Tag der Disputation: Potsdam, 3.Juni 2019

Hauptbetreuer/in: Prof. Dr. Ralph Tiedemann (Universität Potsdam)
weitere Gutachter: PD Dr Thomas Hovestadt (Universität Würzburg), und
Prof. Dr. F.J. Weissing (University of Groningen, The Netherlands)

https://doi.org/10.25932/publishup-43062
https://nbn-resolving.org/urn:nbn:de:kobv:517-opus4-430627

A Gisela, Adelis y Gibran

Con profundo amor y agradecimiento

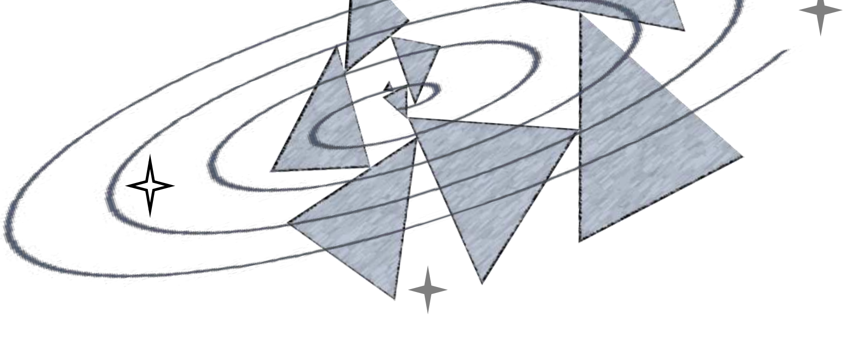


Table of Contents

Summary

A contemporary challenge in Ecology and Evolutionary Biology is to anticipate the fate of populations of organisms in the context of a changing world. Climate change and landscape changes due to anthropic activities have been of major concern in the contemporary history. Organisms facing these threats are expected to respond by local adaptation (*i.e.*, genetic changes or phenotypic plasticity) or by shifting their distributional range (migration). However, there are limits to their responses. For example, isolated populations will have more difficulties in developing adaptive innovations by means of genetic changes than interconnected metapopulations. Similarly, the topography of the environment can limit dispersal opportunities for crawling organisms as compared to those that rely on wind. Thus, populations of species with different life history strategy may differ in their ability to cope with changing environmental conditions. However, depending on the taxon, empirical studies investigating organisms' responses to environmental change may become too complex, long and expensive; plus, complications arising from dealing with endangered species. In consequence, eco-evolutionary modeling offers an opportunity to overcome these limitations and complement empirical studies, understand the action and limitations of underlying mechanisms, and project into possible future scenarios. In this work I take a modeling approach and investigate the effect and relative importance of evolutionary mechanisms (including phenotypic plasticity) on the ability for local adaptation of populations with different life strategy experiencing climate change scenarios. For this, I performed a review on the state of the art of eco-evolutionary Individual-Based Models (IBMs) and identify gaps for future research. Then, I used the results from the review to develop an eco-evolutionary individual-based modeling tool to study the role of genetic and plastic mechanisms in promoting local adaption of populations of organisms with different life strategies experiencing scenarios of climate change and environmental stochasticity. The environment was simulated through a climate variable (*e.g.*, temperature) defining a phenotypic optimum moving at a given rate of change. The rate of change was changed to simulate different scenarios of climate change (no change, slow, medium, rapid climate change). Several scenarios of stochastic noise color resembling different climatic conditions were explored. Results show that populations of sexual species will rely mainly on standing genetic variation and phenotypic plasticity for local adaptation. Population of species with relatively slow growth rate (*e.g.*, large mammals) –

especially those of small size – are the most vulnerable, particularly if their plasticity is limited (*i.e.*, specialist species). In addition, whenever organisms from these populations are capable of adaptive plasticity, they can buffer fitness losses in reddish climatic conditions. Likewise, whenever they can adjust their plastic response (*e.g.*, bed-hedging strategy) they will cope with bluish environmental conditions as well. In contrast, life strategies of high fecundity can rely on non-adaptive plasticity for their local adaptation to novel environmental conditions, unless the rate of change is too rapid. A recommended management measure is to guarantee interconnection of isolated populations into metapopulations, such that the supply of useful genetic variation can be increased, and, at the same time, provide them with movement opportunities to follow their preferred niche, when local adaptation becomes problematic. This is particularly important for bluish and reddish climatic conditions, when the rate of change is slow, or for any climatic condition when the level of stress (rate of change) is relatively high.

Zusammenfassung

Eine aktuelle Herausforderung in der Ökologie und Evolutionsbiologie besteht darin, das Schicksal von Populationen verschiedener Lebewesen im Kontext einer sich verändernden Welt zu antizipieren. Der Klimawandel und die durch anthropologische Aktivitäten verursachten Landschaftsveränderungen sind im Laufe der Geschichte von großer Bedeutung geworden. Von den Organismen, die sich diesen Veränderungen stellen, wird erwartet, dass sie durch lokale Anpassung (d.h. genetische Veränderungen oder phänotypische Plastizität) oder durch Verschiebung ihres Verbreitungsgebietes (Migration) darauf reagieren. Allerdings sind diese Reaktionen begrenzt. So werden beispielsweise isolierte Populationen mehr Schwierigkeiten bei der Entwicklung adaptiver Neuheiten mittels genetischer Variation haben als vernetzte Metapopulationen. Ebenso kann die Topographie der Umgebung die Ausbreitungsmöglichkeiten für zum Beispiel kriechende Organismen im Vergleich zu denen, die auf Wind angewiesen sind, einschränken. So können Populationen von Arten mit unterschiedlichen Lebensstrategien verschiedene Fähigkeiten haben, mit den sich ändernden Umweltbedingungen umzugehen. Empirische Studien, die die Reaktionen von Organismen auf Umweltveränderungen untersuchen, können jedoch, je nach Taxon, zu komplex, langwierig und teuer werden. Ebenso sollten Komplikationen im Umgang mit gefährdeten Arten nicht außer Acht gelassen werden. Die ökoevolutionäre Modellierung bietet jedoch die Möglichkeit, diese Einschränkungen zu überwinden und empirische Studien zu ergänzen, die Wirkung und Grenzen der zugrunde liegenden Mechanismen zu verstehen und mögliche Zukunftsszenarien zu erstellen. In dieser Arbeit untersuche ich mittels einer Modellierungsmethode die Wirkung und relative Bedeutung evolutionärer Mechanismen (einschließlich phänotypischer Plastizität) auf die Fähigkeit zur lokalen Anpassung von Populationen mit unterschiedlichen Lebensstrategien, die Szenarien des Klimawandels durchleben. Dazu habe ich in einem Review den Stand der Technik ökoevolutionärer individuenbasierender Modelle (Individual-Based Models; IBMs) zusammengefasst und Ansätze für eine zukünftige Forschung identifiziert. Die Erkenntnisse des Reviews nutzte ich, um ein ökoevolutionäres, individuelles Modellierungsprogramm zu entwickeln. Dieses analysiert die Rolle genetischer und plastischer Mechanismen zur Förderung der lokalen Anpassung organismischer Populationen mit unterschiedlichen Lebensstrategien, welche Szenarien des Klimawandels und der ökologischen Stochastik erfahren. Die Umweltbedingungen

wurden durch eine klimatische Variable (z.B. Temperatur) simuliert, die ein phänotypisches Optimum definiert, das sich mit einer bestimmten Änderungsrate bewegt. Verschiedene Änderungsraten wurden angewandt, um unterschiedliche Szenarien des Klimawandels darzustellen (keine Veränderung, langsamer, mittlerer, schneller Klimawandel). Es wurden mehrere Szenarien stochastischen Farbrauschens untersucht, die verschiedene klimatische Bedingungen widerspiegeln. Die Ergebnisse zeigen, dass Populationen sexueller Arten hauptsächlich auf genetische Variation und phänotypische Plastizität hinsichtlich lokalen Anpassung angewiesen sind. Populationen von Arten mit relativ langsamer Wachstumsrate (z.B. große Säugetiere), und insbesondere die mit kleiner Populationsgröße, sind am anfälligsten, vor allem wenn ihre Plastizität begrenzt ist (d.h. spezialisierte Arten). Wenn Individuen dieser Populationen zu adaptiver Plastizität fähig sind, können sie Fitnessverluste unter „rötlichen" Klimabedingungen ausgleichen. Zugleich können diese Populationen durch Anpassung der Plastizität auch unter bläulichen Umweltbedingungen zurecht kommen (z.B. Bed-Hedging-Strategie). Im Gegensatz dazu können sich Lebensstrategen mit hoher Reproduktionszahl auf nicht-adaptive Plastizität zur lokalen Anpassung an neue Umweltbedingungen verlassen, es sei denn, die Änderungsrate ist zu schnell. Eine empfohlene Handlungsmaßnahme ist es, die Eingliederung von isolierten Populationen in Metapopulationen zu gewährleisten, so dass die genetische Variation erhöht werden kann. Wenn eine lokale Anpassung problematisch wird, sollte ihnen gleichzeitig Migrationsfreiraum gegeben werden, um ihrer bevorzugten Nische zu folgen. Dies ist besonders wichtig für „bläuliche" und „rötliche" Klimabedingungen, bei denen die Änderungsrate langsam ist, oder für jede klimatische Bedingung, wenn die Belastung (Änderungsrate) relativ hoch ist.

Outline and own contribution

Chapter 1 broadly introduces and connects all topics of research presented in the following chapters and develops the research questions that were investigated. Chapters 2-4 show the products of my investigation in the form of three manuscripts (one published, one submitted and one in preparation), and can be read independently. Below, I also mention my contributions to each of the manuscripts. Chapter 5 provides a general discussion on the overall results of all topics, how they contribute to knowledge, shortcomings, the road ahead, and general conclusions.

In Chapter 2, I conducted a review on the state of the art of individual-based eco-evolutionary models investigating organisms' responses to environmental change (Romero-Mujalli et al. 2018 Reg. Environ. Change J.). In this review, I identified knowledge gaps to motivate future research. Additionally, I used the outcome of this review to develop my eco-evolutionary model, which I used for Chapters 3 and 4. Furthermore, I used my model to teach my own lecture on eco-evolutionary modeling at the University of Potsdam; and it is currently being used as part of a bachelor thesis.

Chapter 3 focuses on local adaptation by means of genetic changes and investigates whether the mutation rate could evolve and increase evolvability of populations of organisms under directional stochastic climate change scenarios (Romero-Mujalli et al submitted). For this research, I used my eco-evolutionary model and developed a new (presumably more realistic) method for the simulation of beneficial mutations based on the concept of slightly deleterious mutations (Ohta 1973; Eyre-Walker et al. 2002). With this method I also tested the effect of the rather common assumption in eco-evolutionary individual-based models of a symmetric distribution (50% chance) for beneficial and deleterious mutations (Romero-Mujalli et al. 2018).

Chapter 4 focuses on the role and relative importance of non-adaptive and adaptive forms of phenotypic plasticity for populations with different life strategy experiencing scenarios of directional stochastic climate change (Romero-Mujalli et al. in prep.). For this research I extended my eco-evolutionary model to simulate non-adaptive and adaptive phenotypic plasticity. So far, most models focus on the adaptive nature of phenotypic plasticity (Via and Lande 1985; Nussey et al. 2007; Lande 2009; Chevin et al. 2010; Lande 2014). For adaptive phenotypic plasticity, I developed and proposed novel methods that accounted for limits to plasticity and simulate plasticity as developmentally constructive (Laland et al. 2015). Limits of plasticity have received little attention in the literature (Murren et al. 2015; Romero-Mujalli et al. 2018). In addition, with this work, I contribute to the understanding of the relative importance of phenotypic plasticity for populations with different life strategy experiencing different climatic conditions (forms of stochasticity) and scenarios of climate change. This last topic has been understudied.

Chapter 1

General Introduction

CHAPTER 1

General Introduction

Evolution in contemporary timescales:

"Nothing in Biology makes sense except in the light of Evolution"

Theodosius Dobzhansky, 1964

"Nothing in Evolutionary Biology makes sense except in the light of Ecology"

Peter and Rosemary Grant, 2008

"Nothing in Evolution or Ecology makes sense except in the light of the other"

F. Pelletier, D. Garant, and A. P. Hendry, 2009

1.1 Eco-evolutionary research study the bidirectional interaction of organisms with their environment

Traditionally, the processes of Ecology and Evolution were assumed to occur in non-overlapping timescales, and therefore, they developed quite independently from each other. Ecological time scales are short, embracing the life time of individual organisms up to few generations. Ecological timescales were assumed too fast for evolution to play a role (*i.e.*, Ecology was assumed to occur in evolutionary stasis). In contrast, evolutionary timescales were assumed long enough, such that ecological interactions could be neglected. However, populations can evolutionarily react faster than expected when they experience changes in their environment. Pioneering research on ecological genetics showed that evolution can occur in ecological-relevant timescales (Ford 1975). Nonetheless, it will be until early 21st century when this notion took more impact on research, especially because of the – still current – urge need in anticipating climate change impacts on biodiversity (Fussmann et al. 2003; Yoshida et al. 2003; Carroll et al. 2007; Fussmann et al. 2007; Hendry 2016b). Furthermore, such "rapid" evolutionary responses can affect and change the ecological interactions, which can then feedback as novel selective pressures for evolutionary change before repeating the loop (Downing 1998). This feedback loop has been called eco-evolutionary dynamics or feedbacks and is the study focus of the recent field of Eco-Evolutionary Biology (Beckerman et al. 2016; Hendry 2016b). It recognizes the double causality and the bidirectionality of interactions (van Gestel and Weissing 2016). The field of eco-evolutionary research is expected to improve our understanding of species' responses to environmental change, such as climate change.

1.2 Empirical evidence for eco-evolutionary dynamics is widespread

Empirical evidence for eco-evolutionary dynamics is widespread and have been reported both, under laboratory conditions (Fussmann et al. 2003; Yoshida et al. 2003; Lohbeck et al. 2012; Matthews et al. 2016) and in the wild (Boag and Grant 1981; Rudman and Schluter 2016). For example, evolution in contemporary timescales in response to density-dependence selection was suggested to drive zooplankton-algae predator-prey dynamics under laboratory conditions (Fussmann et al. 2003; Yoshida et al. 2003). Similarly, adaptive evolution was observed for marine calcifying organisms under artificial scenarios of ocean acidification (Lohbeck et al. 2012). Eco-evolutionary dynamics of the beak size of the Galápagos finch, *Geospiza fortis* (one of the Darwin finches) was observed in the wild in response to changes in the relative abundance of large vs small seeds (Boag and Grant 1981). In this case, the size of the beak determines the efficiency of handling seeds of different size. During dry years, large seeds were more abundant than small seeds, while the converse occurred during wet years. Most empirical eco-evolutionary research has been conducted on organisms with short generation time. Thus, eco-evolutionary dynamics in organisms with complex life cycles and long generation time are yet to be explored (Shefferson and Salguero-Gómez 2015). However, this task can bring up difficulties as experiments may become too complex, long and expensive; plus, complications arising from dealing with endangered species. In consequence, eco-evolutionary modeling offers a good opportunity to complement empirical studies, understand the action and limitations of underlying mechanisms, and project into possible future scenarios.

1.3 Process-based mechanistic models, a promising approach for eco-evolutionary research

A model is an abstract representation of reality that has a purpose (Grimm and Railsback 2005). For example, models can be used to predict the system' behavior in a novel situation or environment; or to understand why the system behaves in the way we observe and not in another different way. There are many modeling approaches. However, those explicitly considering underlying processes and mechanisms for the understanding of system behavior provide a promising avenue for eco-evolutionary research. This is, because they are expected to still maintain predictive power in novel environmental conditions, as compared to models relying on statistical correlations and empirically determined demographic rates (Stillman et al. 2015). This can be critical in eco-evolutionary research because of the uncertainty that a novel environment imposes. Models aiming at this are called process-based mechanistic models (Dunlop et al. 2009).

Examples of eco-evolutionary modeling approaches that have gain popularity for the understanding of population's responses to environmental change are Species Distribution Models, Trait-Based Models, and Individual-Based Models (IBMs). Species Distribution Models strongly rely on statistical techniques to assess species persistence and distribution under scenarios of environmental change (Elith and Leathwick 2009). The strength of their projections largely depends on the validity of their underlying regression models (Merow et al. 2014). Recent approaches have started to include processes (*e.g.*, evolution and dispersal) into Species Distribution Models (Bush et al. 2016). The Trait-Based modeling approach describes distributions of functional traits – and their changes – in terms of their moments (*e.g.*, mean and variance of the distribution) (Merico et al. 2014). Assumptions regarding the shape of such distributions are critical for the resulting eco-evolutionary dynamics (Klauschies et al. 2018). In contrast, in IBMs the properties (or behavior) of the system (*e.g.*, trait dynamics at the population level) emerges from processes, interactions, and adaptive decisions taking place at the fundamental ecological unit (*i.e.*, individuals) (Grimm and Railsback 2005; Romero-Mujalli et al. 2018). Thus, IBMs allow to gain a detailed and direct understanding of the way underlying mechanisms act and affect population dynamics and persistence. Interestingly, a common theoretical observation, independent of the selected modeling approach, is that the inclusion of evolutionary dynamics into ecological models lead to more optimistic model projections of species responses to climate change scenarios (Reed et al. 2011; Bush et al. 2016). However, when exactly do limits to adaptations occur still needs further research (Bell 2013; Kopp and Matuszewski 2014).

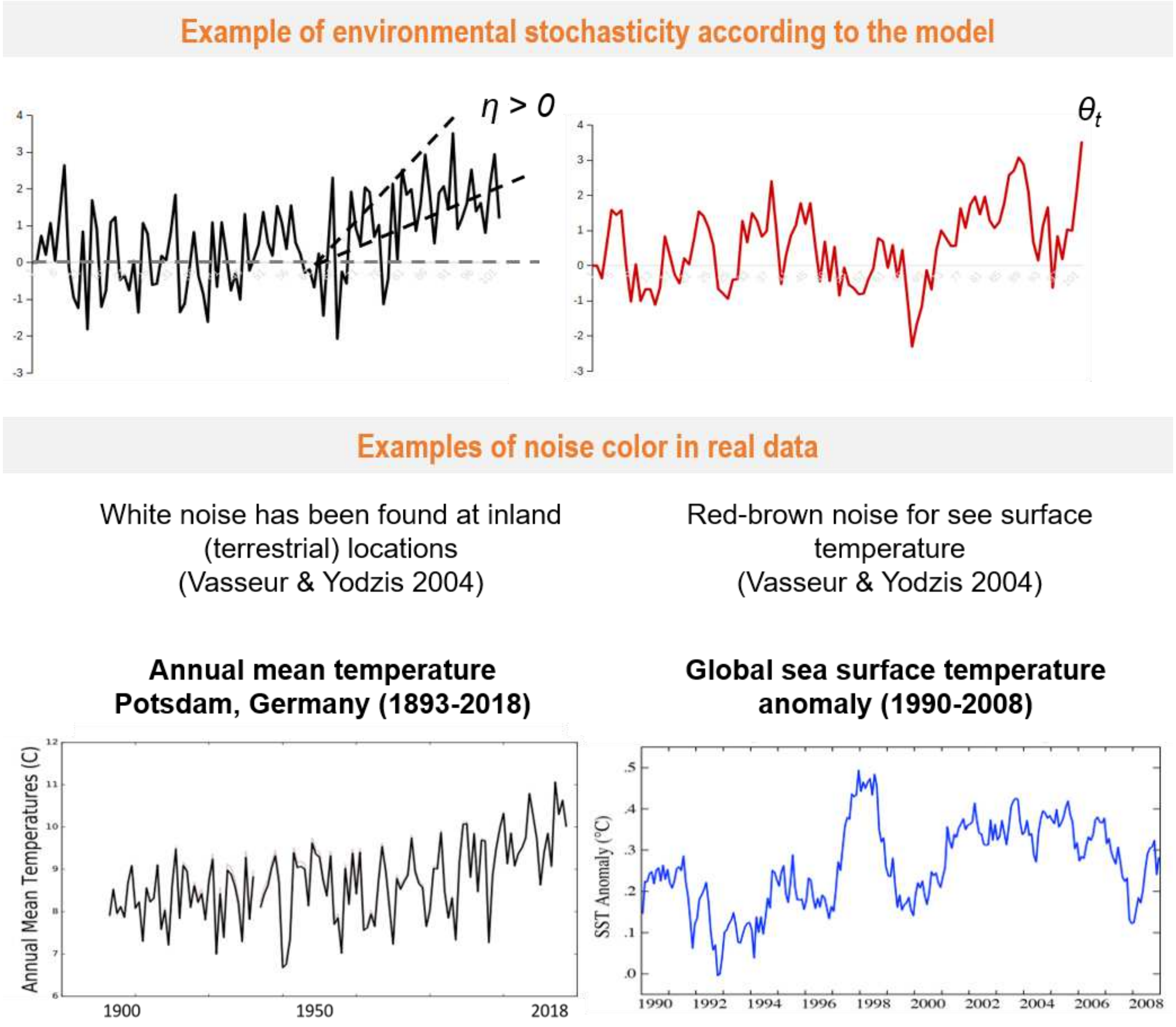
1.4 The modeling approach of this dissertation: an eco-evolutionary IBM

> "Many – perhaps most – of the great issues of science are qualitative, not quantitative, even in physics and chemistry" (Platt 1964)

For the studies shown in Chapter 3 and 4, I developed an eco-evolutionary IBM for the understanding of organisms' responses to different climatic conditions and scenarios of climate change. This approach granted me to explicitly represent evolutionary mechanisms (including phenotypic plasticity); understand their effect on population persistence under different environmental scenarios; and their limits and relative importance for populations of organisms with different life strategy (*e.g.*, mammals *vs* insects; sexual *vs* asexual organisms). This model is being release as a modeling tool along with the publication of Chapter 4. It represents the materialization of joint ideas, own initiative, and teamwork with the PhD candidates that belong to the research school of Adaptive Evolutionary Responses to Rapid Climate Change at the University of Potsdam. Furthermore, this modeling tool was successfully used and tested by students at the University of Potsdam as part of a lecture that I designed and taught on eco-evolutionary modeling during the summer semester 2017.

1.5 Modeling climatic conditions and scenarios of climate change

Models can also be used to project the behavior of a given system into a hypothetical near future (*e.g.*, into scenarios of future IPCC climatic conditions). IPCC stands for Intergovernmental Panel on Climate Change and is the international body responsible to communicate scientific findings related to climate change to policy makers. For my work in this dissertation, I implemented several scenarios of climate change as if they were different IPCC emission scenarios, ranging from no change, to slow, medium, to rapid climate change (see Chapters 3 and 4). In addition, I simulated different climatic conditions according to the form of the fluctuations of the climatic variable. A common approach, which has been regarded best suit to simulate directional climate change environmental scenarios, is the addition of a trend to the mean environmental variable (Kopp and Matuszewski 2014; Vincenzi 2014). Moreover, the addition of stochastic autocorrelated noise around the mean environmental variable allows to simulate different forms – or noise colors – in the fluctuations of the environmental variable (Heino et al. 2000; Schwager et al. 2006; Björklund et al. 2009). The implementation of different stochastic noise color allows to simulate environmental fluctuations as they occur for different habitats and climate variables (*e.g.*, white noise, typical of inland terrestrial locations, and red-brown noise typical of coastal and marine habitats, Vasseur and Yodzis 2004) (Fig. 1.1). More details can be found in the methods described in Chapter 3 and 4.


Example of environmental stochasticity according to the model

Examples of noise color in real data

White noise has been found at inland (terrestrial) locations (Vasseur & Yodzis 2004)

Red-brown noise for see surface temperature (Vasseur & Yodzis 2004)

Fig. 1.1 Examples of environmental fluctuations (noise color) according to the model used for the studies in this dissertation (upper plots), and of time series of real temperature data (plots below). An anomaly is a departure from average conditions. The parameters η and ϑ_t indicated the rate of environmental change and the environmental variable (in this case, temperature), respectively. Varying the parameter η allows simulating different scenarios of climate change (*e.g.*, no change $\eta = 0$, slow, medium, to rapid climate change). Source: https://data.giss.nasa.gov/

1.6 Populations can respond to changes in their environment by local adaptation or by shifting their distributional range

According to some studies, climate-related local extinctions have already been reported and are widespread among plant and animal species (Wiens 2016). Particularly, they have been more prevalent in tropical than temperate regions, and among freshwater taxa, as compared to terrestrial and marine species (Wiens 2016). Furthermore, several studies also report shifts in geographical distributions of populations towards higher latitudes and elevations (Moritz and Agudo 2013), and in their phenology (Jenni and Kéry 2003; van Buskirk et al. 2009; Visser et al. 2012). A better understanding of how populations of species respond to changing climatic conditions can help to identify mechanisms of conservation that promote persistence. Populations of species experiencing environmental change are expected to respond either by local adaptation, by passive or active shift of their distributional range, or by local extinction (Franks et al. 2014; Wiens 2016). This dissertation focus on the ability of populations to locally adapt to novel environmental conditions. Therefore, dispersal (movement) potentially leading to range shift will be slightly covered (Chapter 3). The project BioMove at the University of Potsdam extensively covers and investigates the process of dispersal potentially leading to shifts in the distributional range of species.

1.7 Local adaptation occurs by either genetic changes or phenotypic plasticity

Novel environmental conditions impose selective pressures on populations towards the creation of fitter alternative phenotypes. This need for local adaptation becomes particularly relevant for populations of organisms with limited movement opportunities, or for those reaching novel environmental conditions at the front of the expanding range (*e.g.*, during invasions, Wright et al. 2010; Cobben et al. 2017). Adaptive phenotypic innovations in response to novel local environmental conditions can occur either, by genetic changes or phenotypic plasticity. The ability of populations to genetically respond to novel environmental conditions depends, among other factors, on the population size and the supply of useful genetic variation (Gonzalez et al. 2013). Typically, large populations are more likely to possess higher evolvability potential in the form of both, standing genetic variation (*e.g.*, more extreme individuals) and de-novo mutations, than small populations (Burger and Lynch 1995; Bell 2013; Romero-Mujalli et al. 2017). Evolvability is defined as the capacity of lineages to adapt to changing conditions (Futuyma et al. 2005). Similarly, in sexual species, higher evolvability is expected in populations of organisms with relatively high fecundity (in terms of average number of offspring per reproductive couple) and therefore, faster population growth rate (Björklund et al. 2009). Interconnected metapopulations can benefit from the input of new genetic variation via immigration, and hence, experience a larger effective gene pool as compared to isolated populations (Lakovic et al. 2017). Thus, the presence of corridors connecting metapopulations can enhance the chance for evolutionary rescue. This is, the chance that populations will adapt and persist environmental conditions that would have been lethal to their ancestors (Bell 2013).

At a microscopic level, polygenic characters, typical of quantitative traits, slow down the reduction in genetic variance in response to selection (Bulmer 1971; Lynch and Walsh 1998). Polygenic characters are composed of several loci, each contributing to variation in the phenotypic trait (Lynch and Walsh 1998; Futuyma et al. 2005). The process of recombination in sexual species can sort out the genetic variance present in polygenic characters and potentially speed up the process of adaptation, without the need of de-novo mutations (Marais and Charlesworth 2003). Mutations are the ultimate source of variation and are considered a rare event (Futuyma et al. 2005). Recent studies on populations' responses to stressful climatic conditions have investigated whether elevated mutation rates can arise in these populations and increase their evolvability (*e.g.*, Clark et al. 2011; Cobben et al. 2017). One of them, contrary to the current paradigm, found that elevated mutation rates can contribute to range expansion in populations of sexual species (Cobben et al. 2017). The current paradigm holds that the mutation rate will be kept low, limited either, by the cost of fidelity or by the drift limit (Lynch 2011; Martincorena and Luscombe 2013). Furthermore, it states that it will not evolve to elevated rates, unless mutator loci affecting the mutation rate can hitchhike with beneficial mutations at other loci (Shaver et al. 2002). Following the findings in Cobben et al. (2017), it is worth asking whether the mutation rate can also evolve and increase evolvability of populations of sexual species under climate change scenarios. This is the topic of chapter 4.

On the other hand, phenotypic plasticity can provide a faster response than genetic changes and can buffer fitness losses of populations experiencing novel environmental conditions (Lande 2009; Reusch 2014). Phenotypic plasticity is defined as any non-genetic change of the phenotype induced by novel environmental conditions (West-Eberhard 2003; Pigliucci 2005; Reusch 2014; Laland et al. 2015). Plastic adjustments of the phenotype can occur within the life span of an organism, or between generations (transgenerational plasticity) (Galloway and Etterson 2007). Additionally, plasticity can be fixed during ontogeny (constant character) as in developmental plasticity (Lande 2014; Romero-Mujalli et al. 2018), or flexible when it can reversibly change depending on environmental conditions (*e.g.*, physiological and behavioral traits) (Lande 2014; Romero-Mujalli et al. 2017).

For modern Biology, phenotypic plasticity was considered as nuisance since the rediscovery of Mendel’s laws until late 20th century, when it became integral part of organisms’ responses to their environment (Pigliucci 2005). The most common modeling approach for plasticity is the linear reaction norm (Via and Lande 1985; Chevin et al. 2010; Ashander et al. 2016; Romero-Mujalli et al. 2018), though, in nature, it can take any shape (Murren et al. 2014). A non-flat (*i.e.*, plastic) norm of reaction in a population exposed to changing environmental conditions is assumed to be present due to past selection (Via and Lande 1985; Lande 2009). Alternatively, phenotypic plasticity can evolve in populations in response to changing environmental conditions, particularly, when cues are reliable and costs negligible (Ghalambor et al. 2007). Though, most studies have focused on adaptive phenotypic plasticity (Lande 2009; Lande 2014; Ashander et al. 2016), it can also be maladaptive (Ghalambor et al. 2007; Hendry 2016a).

Since perfect phenotypic plasticity has not been observed in nature, costs and limits to plasticity muss exists (DeWitt et al. 1998; Pigliucci 2005). Costs to plasticity arise due to energetic expenses in the development of an optimum plastic response, while limits refer to the impossibility to produce an optimal phenotype (DeWitt et al. 1998; Pigliucci 2005). Most modeling studies have assumed costs to plasticity to prevent perfect plasticity from arising. However, empirical studies have not detected significant costs to plasticity (Murren et al. 2015), especially when dealing with developmental plasticity or constant characters. Flexible characters are assumed to be costlier than constant characters in order to maintain the machinery that makes this kind of plasticity possible (Lande 2014). In contrast, models implementing explicit limits to phenotypic plasticity have received little attention in the literature (Murren et al. 2014; Romero-Mujalli et al. 2018) and represents a niche for future research.

The characteristics of the environmental change (*e.g.*, environmental stochasticity) can also affect the evolution of plasticity (Reed et al. 2010; Ergon and Ergon 2016; Ashander et al. 2016). Most of these studies focus on stochastic fluctuations in environmental cues and their correlation (of the cues) with the environmental optimum. Studies exploring the effect of phenotypic plasticity on population persistence under different climatic conditions (*i.e.*, different forms of the stochastic noise) and scenarios of climate change is lacking. Furthermore, the relative importance of phenotypic plasticity promoting persistence of populations with different life history strategy have received little attention as well. Finally, a recursive question in the literature is whether adaptive phenotypic plasticity promotes or hinder evolution (Ghalambor et al. 2007; Hendry 2016a). All these research topics are addressed in Chapter 4.

1.8 Aims of this study

The main objectives of this study were (1) to perform a literature review on the state of the art of eco-evolutionary individual-based models and, in this, identify knowledge gaps, and (2) to investigate the effect and relative importance of evolutionary mechanisms (including phenotypic plasticity) on the ability for local adaptation of populations with different life strategy experiencing climate change scenarios. Chapter 2 (the literature review) contributed to the development of the modeling tool. Chapter 3 and 4 used the modeling tool and focused on the role of genetic properties and phenotypic plasticity on the local adaptation ability of populations, respectively.

Main research questions and hypothesis that were investigated per Chapter

Chapter 2	**Research question 1**	What is the state of the art of eco-evolutionary IBMs?
	Research question 2	What are the gaps to motivate future research?
Chapter 3	**Research question**	Can the mutation rate evolve to elevated values and increase evolvability of populations of sexual species under climate change scenarios?
	Hypothesis	The mutation rate can evolve to elevated rates if they can hitchhike to beneficial mutations at other loci (strong linkage, typical of asexual organisms). From this hypothesis, it follows that elevated mutation rates are unlikely to evolve in sexual species.
Chapter 4	**Research question 1**	What is the effect of adaptive and non-adaptive phenotypic plasticity on population persistence under climate change scenarios?
	Hypothesis 1	If organisms can respond in the direction of the optimum through adaptive phenotypic plasticity, populations of organisms relying on this form of plasticity will experience higher probability of persistence than those relying on non-adaptive phenotypic plasticity in all environmental scenarios.
	Research question 2	What is the relative importance of forms of plasticity for populations with different life strategy?
	Hypothesis 2	Given that populations can buffer fitness losses in novel environmental conditions through phenotypic plasticity, then plasticity will be more important increasing probability of persistence for those populations in which individuals are limited to produce relatively few offspring than those with individuals with higher fecundity.

Chapter 2

Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions

CHAPTER 2

Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions

Daniel Romero-Mujalli[1,2], Florian Jeltsch[2,3], and Ralph Tiedemann[1]

This Chapter is published in:

Regional Environmental Change Journal

doi: 10.1007/s10113-018-1406-7

[1] University of Potsdam, Evolutionary Biology/Systematic Zoology, Karl-Liebknecht-Strasse 24-25, 14476 Potsdam, Germany

[2] University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlenberg 3, 14476 Potsdam, Germany

[3] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany

2.1 Abstract

A challenge for eco-evolutionary research is to better understand the effect of climate and landscape changes on species and their distribution. Populations of species can respond to changes in their environment through local genetic adaptation or plasticity, dispersal, or local extinction. The individual-based modelling (IBM) approach has been repeatedly applied to assess organismic responses to environmental changes. IBMs simulate emerging adaptive behaviors from the basic entities upon which both ecological and evolutionary mechanisms act. The objective of this review is to summarize the state of the art of eco-evolutionary IBMs and to explore to what degree they already address the key responses of organisms to environmental change. In this, we identify promising approaches and potential knowledge gaps in the implementation of eco-evolutionary mechanisms to motivate future research. Using mainly the ISI Web of Science, we reveal that most of the progress in eco-evolutionary IBMs in the last decades was achieved for genetic adaptation to novel local environmental conditions. There is, however, not a single eco-evolutionary IBM addressing the three potential adaptive responses simultaneously. Additionally, IBMs implementing adaptive phenotypic plasticity are rare. Most commonly, plasticity was implemented as random noise or reaction-norms. Our review further identifies a current lack of models where plasticity is an evolving trait. Future eco-evolutionary models should consider dispersal and plasticity as evolving traits with their associated costs and benefits. Such an integrated approach could help to identify conditions promoting population persistence depending on the life history strategy of organisms and the environment they experience.

Keywords

Modeling; individual-based models; Ecology; Evolution; eco-evolutionary dynamics

2.2 Introduction

The most pressing contemporary challenge in ecology and evolutionary biology is to understand and predict how species cope with increasing rates of environmental change (Chevin et al. 2010; Gonzalez et al. 2013). Particularly challenging is to disentangle the combined (possibly synergistic) effects of climate and landscape changes (Brook et al. 2008; Jeltsch et al. 2011). Populations of organisms facing these perturbations are expected to respond either by local genetic adaptation or plasticity, an active or passive shift of the distributional range, or (local) extinction (Boutin and Lane 2014; Franks et al. 2014; Wiens 2016).

The field of eco-evolutionary research can significantly contribute to our understanding of organisms' responses to such environmental changes on ecological relevant time-scales (for recent reviews see Boutin and Lane 2014; Charmantier and Gienapp 2014; Collins et al. 2014; Crozier and Hutchings 2014; Franks et al. 2014; Schilthuizen and Kellermann 2014; Stoks et al. 2014; Urban et al. 2014). In particular, modelling approaches can be helpful in unraveling the complexity of such dynamics, for example when experiments are too complex, focal species are endangered, or generation times of the focal organisms are too long (Boutin and Lane 2014; Shefferson and Salguero-Gómez 2015). Traditional ecological modelling approaches have often assumed equivalent conspecific individuals (Bolnick et al. 2011), i.e., populations with ubiquitous invariable traits under evolutionary stasis. However, the realization that organisms can respond adaptively to a changing world also on ecological time-scales has challenged the traditional ecological modelling approach (Boag and Grant 1981; Yoshida et al. 2003). For example, Fussmann et al. (2003) found that their ecological model of zooplankton (i.e., rotifers) correctly predicted the observed populations trajectories only by including phenotypic changes.

Eco-evolutionary models need to consider both how exactly environments are expected to change and how organisms potentially respond (Crone et al. 2013). In this, they need to address all possible adaptive responses of organisms, including local adaptation by genetic changes, plasticity, and dispersal. So far, most models attempting to understand and predict possible organismal responses to environmental change fall into two categories: (i) species, niche or habitat distribution models (also called climate envelope models) and (ii) process-based models. Species distribution models are based on statistical techniques to assess species persistence and expected distribution (range shift) as a consequence of environmental change (Elith and Leathwick 2009). Thus, the strength of their projections relies on the validity of the underlying regression models (Merow et al. 2014). In contrast, process-based (also called mechanistic) eco-evolutionary models combine processes of evolutionary genetics and demography to predict, for example, the conditions under which populations can maintain positive intrinsic growth rate in the presence of environmental change (Dunlop et al. 2007; Dunlop et al. 2009; Chevin et al. 2010). Process-based models typically require more parameters, but need less calibration data and can lead to a relatively "deeper" understanding of underlying eco-evolutionary dynamics because of the explicit simulation of processes and mechanisms involved in the dynamics of organismal responses to environmental change (Jeltsch et al. 2008; Dunlop et al. 2009; Ayllón et al. 2016). Pioneering approaches have already started to link these two modelling approaches for the understanding of species responses to climate change scenarios at a regional spatial scale (see Kearney et al. 2009; Mokany et al. 2015; Bush et al. 2016).

As natural selection acts on the phenotype of individuals, models that simulate entire populations as the basic entity might encounter difficulties in realistically simulating trait variation over time. This limitation can be overcome by individual-based models (IBMs), a specific type of process-based models that has gained much interest in eco-evolutionary research (DeAngelis and Mooij 2005; Dunlop et al. 2007; Dunlop et al. 2009; DeAngelis and Grimm 2014). An important advantage of IBMs is that they capture the adaptive behavior of individuals (i.e., the ecological fundamental units) which is ultimately governing population trait dynamics (DeAngelis and Grimm 2014). In addition, the ecological and evolutionary modules can be linked into a feedback loop, where individual genetic differences produce phenotypic variation as material for selection (Downing 1998). The modelling of eco-evolutionary feedbacks is not an exclusive feature of IBMs. An example of another modeling approach widely used to account for this linkage is the trait-based, adaptive dynamic model (review in Litchman and Klausmeier 2008; Merico et al. 2014). Both the environment and the ecological interactions affect the fitness of phenotypes, which consequently feed back to the genetic component inducing evolutionary genetic change (Downing 1998). IBMs can maintain predictive power also in novel environments (Stillman et al. 2015). This is an additional advantage of IBMs over modelling methods based on empirical relationships to determine demographic rates. All this makes IBMs an attractive approach for eco-evolutionary research on the impact of environmental change (see Dunlop et al. 2009).

After approximately two decades of eco-evolutionary IBMs, we evaluate the progress of this approach entailed in understanding how eco-evolutionary dynamics affect adaptations of organisms in response to environmental change. Reviewing relevant literature from this period, we (1) summarize the state of the art of eco-evolutionary IBMs used to investigate organisms' responses to environmental change, (2) explore to what degree these IBMs already address the possible key responses of organisms to environmental change (i.e., genetic adaptation, plasticity, dispersal), and, (3) reveal approaches and gaps in the implementation of plasticity and its evolution as an important but yet underexplored response in the context of environmental change (Hendry 2016). Based on these analyses we derive recommendations for future directions in the use of IBMs in eco-evolutionary research.

2.3 Methods

2.3.1 Literature search

In order to identify studies using IBMs and investigating eco-evolutionary responses of organisms to environmental change, a search was conducted using the ISI Web of Science. Since one of the interests of this review was environmental change, the search was restricted to papers considering some kind of change in the environment organisms experienced, such as climate change, changes in resource availability, and land use. We also included fragmented landscapes and environmental gradients. The search embraced title and content, and the keywords used were [individual-based or agent-based] and [model*] and [ecol* evol* or eco-evol*] and [environment* change or climate change or fragment* or gradient or land use or degrad*]; and the publication dates considered were from the year 1980 to 2017. Reviews, empirical work, other models than IBMs, and IBMs using only a non-changing environmental condition were excluded. Some articles used the phrase “individual-based model” but were not articles on IBMs. In several cases they were empirical studies recommending IBMs for future research. Often, no environmental change was considered neither. Cited references in the selected literature were also evaluated and included if our selection criteria were met. Subsequently, we applied a predefined list of criteria to extract key information and to characterize the selected literature (Table 2.1).

Table 2.1 List of criteria used to extract information from the selected literature

Criterion	Explanation
Number and kind of species	The taxon (including whether the species is real or unspecified)
Type of species interaction	intra/inter-specific competition, victim-exploiter interactions, mutualism, or commensalism
Reproduction	Sexual or asexual
Mating pattern: mating system	random or non-random (e.g., assortative): polygamy or monogamy
Representation of space	non-spatial, implicit or explicit
Temporal scales	time-scale in generations, years, days, or simulated time-steps
Environmental feedback	Environmental feedback occurs when organisms modify environmental states and, therefore, change selection conditions, subsequently impacting themselves, the environment, and other organisms. Based on niche construction theory (Laland et al. 1999)
Type of environmental change	Change in time and/or space
Evolving traits	Number and type of evolving trait
Type of response	Classifying the evolving trait as related to plasticity, genetic adaptation or range shift
Ploidy level	Haploid or diploid
Neutral genes	Does the model implement genes not subject to selection (e.g., microsatellites)
Number of loci	Total number of loci
Loci effect	Quantification of loci effect
Mutation mode	How genes mutate
Mutation probability	The implemented mutation rate
Inheritance system	How inheritance is implemented
Recombination?	Yes/No
Fitness/Selection	How fitness was calculated?
Is plasticity implemented?	If yes, then, how?
Is plasticity evolving?	Yes/No

2.3.2 State of the art

The state of the art of IBMs for eco-evolutionary research in the context of environmental change was assessed according to the predefined list of criteria (Table 2.1). It was mainly focused on describing key information from the ecological and genetic components of the eco-evolutionary IBMs. The genetic component was further split into explicit and implicit genetics to emphasize the distinction between these two approaches. Our assessment of the state of the art also included how some features of the eco-evolutionary IBMs were implemented, and the number of papers addressing any feature. This information may help researchers to select among methods of implementation and to identify potential gaps of knowledge.

2.3.3 Organisms' expected responses

Since organisms are expected to respond to environmental change by dispersal (potentially causing range-shift of the population), plasticity or local genetic adaptation, we investigated the number of articles accounting for the interplay among these three responses. This was done based on the criterion "Type of response" (Table 2.1). This criterion indicated what kind of response was considered as an evolving trait in the model (i.e., whether the evolving trait was related to the amount or degree of plasticity, whether it could potentially affect range shift, or whether it was related to local genetic adaptation). The number of papers accounting for each expected response was counted. The use of an evolving trait for genetic adaptation is self-evident, while plastic and range shifting responses may well be described as dynamic ecological responses without considering an evolutionary component. However, their inclusion as evolving traits can add, for example, to the understanding of what type of response will be preferred by organisms with given life history constrains and under given environmental context. Through the use of multiple evolving traits, the adaptive response of the population will therefore be treated as an emergent property of the simulated system, following the idea in Dunlop et al. (2009).

2.3.4 Implementation of plasticity

The implementation of plasticity in the selected literature was characterized and the approaches considering the evolution of plasticity (if any) were identified. Phenotypic plasticity was defined as "… the capacity of an organism [with a given genotype] to change its phenotype in response to the environment" (Laland et al. 2015). This definition was selected because it encompasses most of the reported mechanisms of phenotypic plasticity, as for example, epigenetics, maternal effects, learning, environmental induction, acclimation, developmental plasticity, and random noise (West-Eberhard 2003; Hendry 2016). Random noise refers to the part of plasticity that cannot be assigned to a specific measured environmental variable (West-Eberhard 2003). Additionally, phenotypic plasticity was further split into fixed during ontogeny (or constant character), and flexible (or labile character), based on Lande (2014). Phenotypic plasticity was considered fixed during ontogeny or a constant character when the resulting mature phenotype could not be further modified by the environment after a brief critical period early in life (Lande 2014). As a consequence, the resulting mature phenotype is independent of the environmental optimum and cannot be further shaped by the direct experience of the environment. In contrast, flexible or labile plasticity occurs when the phenotype of an individual fluctuates continuously and reversible throughout its life (Lande 2014).

2.4 Results

The number of papers using IBM for eco-evolutionary research has increased from 20 papers before the year 2000 up to 417 until 2017 (web of science, keywords: individual-based model* ecol* evol*). After searching for the keywords (see methods), our database consisted of 135 papers. This database was further reduced by removing articles that were reviews, purely empirical work, other models than IBMs, or IBMs using only a non-changing environmental condition. After cleaning up, our database consisted of 57 remaining papers that were used for the analysis.

2.4.1 State of the art of eco-evolutionary IBMs

Ecology component

Most eco-evolutionary IBMs were spatially explicit and 2D, and used a time scale of generations (see Table 2.2 for details). Models focusing on local adaptation were often non-spatial. Only one study accounted for environmental feedbacks (niche construction). Models of real species were mainly focused on invertebrates, fish and plants, though most models dealt with non-specified or generic species. Most models were focused on one species and competition was the most common type of ecological interaction. In models of sexual organisms, the most frequent mating system was lottery polygyny, and the most common mating pattern was random mating. Assortative mating was common in models focusing on speciation.

Genetic component

Two main different approaches to simulate genetics were identified: explicit and implicit (Table 2). In most models, mutations were assumed to occur with relatively small probability (≤ 1%). In two cases the mutation probability was implemented as evolving trait and subject to evolution by natural selection (Clark et al. 2011; Cobben et al. 2017). The use of a normal distribution was a very common mutation mode for simulating the effect size of mutations, particularly when using implicit genetics based on the infinitesimal model of quantitative genetics. Here, the genetic variance of the distribution constrains the effect size of mutations. Some models considered constant genetic variance. “Stepwise” mutation mode was used when implementing microsatellites as neutral loci. Most of the studies used clonal inheritance with small probability of mutation, which assumes asexual, haploid organisms. On the other hand, studies assuming diploid organisms used mainly alleles or allele values picked randomly per parent per locus (biparental inheritance with complete recombination, i.e., without linkage among any pair of loci).

Table 2.2 Summary of selected key information derived from the application of the predefined criteria on the selected papers. The information was split into the two components that compose eco-evolutionary dynamics: Ecology and Genetics; and Genetics was further separated into explicit and implicit. Plasticity was assumed as an independent component.

Component		Features	Key information	Papers (%)	Reference
Ecology		Nr of species; type of ecological interaction	Modelling of one species, only including intraspecific competition	45 (78.9)	1,2,6-9,11-15,18-24,26-28,30-33,35-38,40-42,44-56
			Modelling of more than one species including additional ecological interactions	5 (8.7)	4,10,25,34,43
		Time scale	Assumed time scale of generations. This occurred particularly when the species was not specified	19 (33.3)	5,8,10,12,15,16,19,22,23,29-31,37,40,41,45, 53,54,56
			For real species, a time scale of years was common	9 (15.8)	1,32,38,44,48,47,49,50,51
		Space	Spatially explicit and 2D models	29 (50.9)	5-8,10,13-15,19,21,23,24,26,29-31,34-36,39-42,49,52, 54-57
			Non-spatial models focused on local adaptation only	11 (19.3)	9,11,18,27,44-48,50,53
		Environmental feedback	Modelling of environmental feedback or niche construction	1 (1.8)	35
		Reproduction	models of sexual species and random mating	22 (38.6)	1,22,23,28,32-35,38,40,41,43-47,49-51,53,54,56
			Assortative mating in models of speciation	4 (7.0)	2,3,5,29
			Lottery polygyny	12 (21.1)	2,3,5,8,16,22,33,38,49,53,54,56
			Promiscuity (typical in models of fish species)	7 (12.3)	1,25,41,44,45,50,52
			Seasonal monogamy	2 (3.5)	46,47
		Fitness	Implicit fitness function was common when modelling real species	19 (33.3)	1,3,9,11,18,20,28,32,34,35,38,43,44,47-52
			Fitness functions that explicitly involved the evolving trait(s) were used when modelling generic species	15 (26.3)	8,12,19,22,27,30,31,39-41,45,46,53,54,56
			Typically, in models of dispersal the evolving trait was not related to fitness, survival or fecundity	8 (14.0)	4,7,17,21,23,26,33,36
Genetics	Explicit	Nr of evolving traits	Modelling one or two evolving traits	41 (71.9)	1,4,6-9,12-15,17-28,30,31,33,35,36,38-40,44-50,52,53,55,56
			Models with ≥10 evolving traits	4 (7.0)	5,34,42,43
		Nr of loci per evolving trait	Modelling of only one locus	22 (38.6)	7,10-15,17-19,23,26,27,30,31,33,34,36-38,40,54
			Some studies modelled several loci (≥ 10)	14 (24.6)	3,8,20-22,28,39,41,43,44,46,50,56,57
		Neutral genes?	Some studies implement neutral loci	7 (12.3)	2,5,15,38,41,52,54

	Mutation probability	Relatively small values (≤ 1%)	33 (57.9)	2,3,5,7,8,10,11,13-23,27,30-33,36-40,42,46,50,53,55
	Mutation mode	Stepwise mutation mode for microsatellites	4 (7.0)	2,5,41,50
		Flip between two alternative alleles	11 (19.3)	2,5,8,16,20,21,32,38-40,57
		In the ‘random-normal’ approach, the effect size of the mutation is constrained by the variance of the distribution, usually assumed to be small and constant	7 (12.3)	3,26,30,31,54-56
		Random reset of gene value according to a uniform distribution involved high effect size	6 (10.5)	11,12,17,18,27,40
	Ploidy level	number of models implementing haploid or diploid organisms	Diploid: 19 (33.3) Haploid: 23 (40.4)	Diploid: 2,3,5,8,16,22,23,28,32,33,38,41,43,44,46,50,53,54,56 Haploid: 7,9-15,17-21,26,30,31,36,37,39,40,42,55,57
	Inheritance and recombination	Clonal inheritance	27 (47.4)	6,7,9-15,17-21,26-31,36,37,39,42,48,55,57
		In models assuming diploid organisms (biparental inheritance), offspring randomly inherited one allele or allele value per parent per locus	17 (29.8)	2,3,8,16,22,23,32-35,41,43,44,46,50,53,56
Implicit	Nr of evolving traits	One or two traits	6 (10.5)	1,25,45,47,49,52
		More than two evolving traits were rare	1 (1.8)	51
	Nr of loci	Implicit infinite (core assumption of the method)	7 (12.3)	1,25,45,47,49,51,52
	Loci effect	Implicit additive (core assumption of the method)		
	Mutation probability	One (core assumption of the method)		
	Mutation mode	Traits are inherited with random deviation according to a normal distribution. The effect size was constrained by the genetic variance (variance of the distribution)		
	Inheritance and recombination	Inheritance was based on the infinitesimal model. Recombination was assumed to be implicit		
	Ploidy level	Not specified		
Plasticity	Implementation	models that did not include plasticity	34 (59.6)	2-8,10-13,15-21,23,26,29-38,41,42,54,56
		Random noise effect on development	11 (19.3)	1,22,28,39,45,46,48-50,52,53
		Reaction-norm	5 (8.8)	25,43,47,51,52
		Learning	4 (7.0)	9,27,40,57
		Plasticity as an alternative strategy with regard to resource or density	4 (7.0)	14,24,44,55

	Costs and limits of plasticity	Explicit costs in the production of plasticity	2 (3.5)	25,27
		Inherent limits to express an optimal phenotype	7 (12.3)	9,14,40,43,47,51,57
	Evolution of plasticity	Plasticity was an evolving trait in few models only	7 (12.)	9,25,27,40,43,47,51

References:

Reed et al. 2011 (1); Sadedin et al. 2009 (2); Aguilée et al. 2013 (3); Barraquand and Murrell 2012 (4); Birand et al. 2012 (5); Bocedi et al. 2014 (6); Bonte et al. 2010 (7); Bridle et al. 2010 (8); Campos et al. 2008 (9); Chaianunporn and Hovestadt 2012 (10); Clark et al. 2011 (11); Downing 1998 (12); Dytham 2009 (13); Dytham et al. 2014 (14); Fronhofer et al. 2012 (15); Gilman and Behm 2011 (16); Green 2009 (17); Griebeler et al. 2010 (18); Haller et al. 2013 (19); Hanski and Heino 2003 (20); Heino and Hanski 2001 (21); Holt and Barfield 2011 (22); Kubisch et al. 2010 (23); Moustakas and Evans 2013 (24); Nonaka et al. 2014 (25); North et al. 2011 (26); Acerbi et al. 2012 (27); Oddou-Muratorio and Davi 2014 (28); Golestani et al. 2012 (29); Guttal and Couzin 2010 (30); Phillips 2012 (31); Picó et al. 2009 (32); Poethke et al. 2011 (33); Haythorne and Skabar 2013 (34); Schweitzer et al. 2014 (35); Travis et al. 2010 (36); Travis et al. 2012 (37); Zheng et al. 2009 (38); Urban and De Meester 2009 (39); Katsnelson et al. 2012 (40); Rebaudo et al. 2013 (41); van der Post and Semmann 2011 (42); Moya-Laraño et al. 2012 (43); Wang and Höök 2009 (44); Björklund et al. 2009 (45); Vincenzi 2014 (46); Dunlop et al. 2007 (47); Vincenzi et al. 2014 (48); Vincenzi and Piotti 2014 (49); Jager 2001 (50); Thériault et al. 2008 (51); Ayllón et al. 2016 (52); Barfield and Holt 2016 (53); Cobben et al. 2017 (54); Fronhofer et al. 2017 (55); Gilbert and Whitlock 2017 (56); Romero-Mujalli et al. 2017 (57)

2.4.2 Organisms' expected responses

No models were found to simultaneously include the three potential eco-evolutionary responses of organisms to environmental change as evolving traits: the evolution of plasticity to facilitate adaptation to variable and changing conditions, the evolution of traits related to dispersal which potentially facilitate range shift, and genetic adaptation related to novel local environmental conditions (Fig. 2.1). Most models have primarily focused on the use of evolving traits related to genetic adaptations to the local environment, followed by the implementation of evolving traits related to dispersal to study populations' range shift in response to environmental change (21 papers, Fig. 2.1). Relatively few papers accounted for the evolution of plasticity (7 papers, Fig. 2.1).

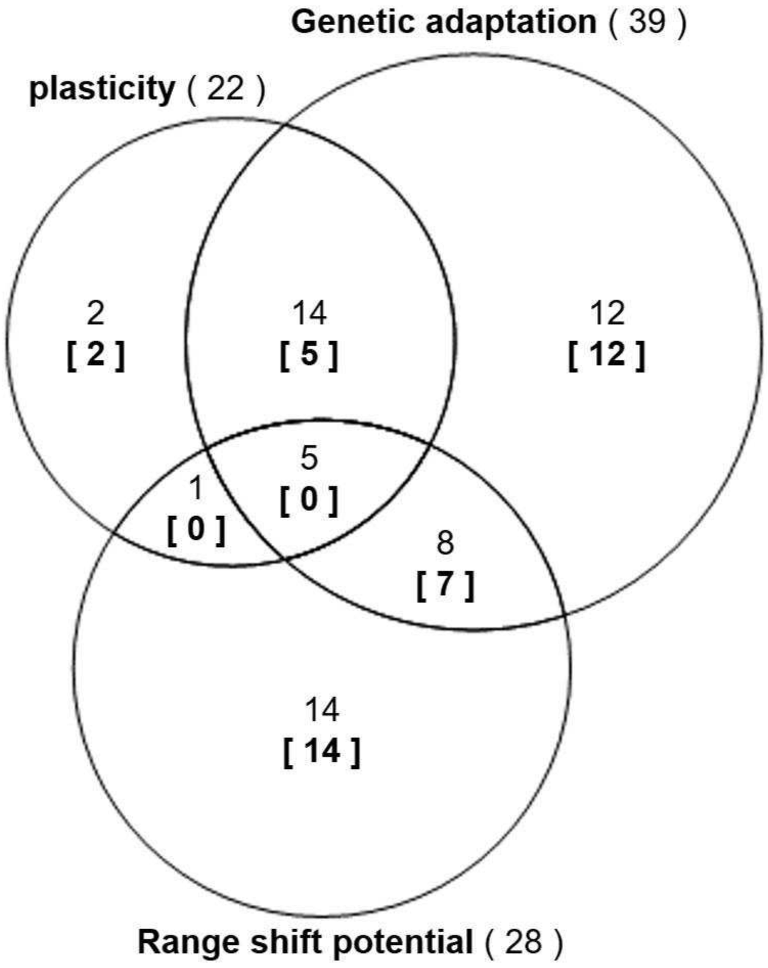


Fig. 2.1 Venn diagram showing the number of papers that implemented local genetic adaptation (genetic adaptation), and/or Plasticity (with or without evolution), and/or Range Shift Potential (with or without evolution on dispersal). The number of papers that implemented as evolving traits the amount or degree of plasticity, or traits that could potentially cause range shift is shown inside brackets. Naturally, local genetic adaptation always involved the use of an evolving trait. The total number of papers per category is shown inside parenthesis. The venn diagram was drawn using the Venn Diagram Plotter of https://omics.pnl.gov/software/venn-diagram-plotter.

2.4.3 Implementation of Plasticity

Plasticity was implemented as a fixed or constant character, when plasticity was given by a reaction-norm, or as a random deviation of the phenotype from genotypic trait value, corresponding to a random environmental effect on development (Fig. 2.2). In other models, plasticity was implemented to be flexible or labile, i.e., plasticity allowed organisms to continuously respond to the environment. Examples of flexible plasticity were learning, and alternative behavioral strategies regarding resource availability and density of conspecifics (Fig. 2.2). The most common implementation of plasticity was random environmental effect on development (n=10, Table 2.2). If plasticity was implemented as an evolving trait, the mechanisms were reaction-norms and learning (Fig. 2.2).

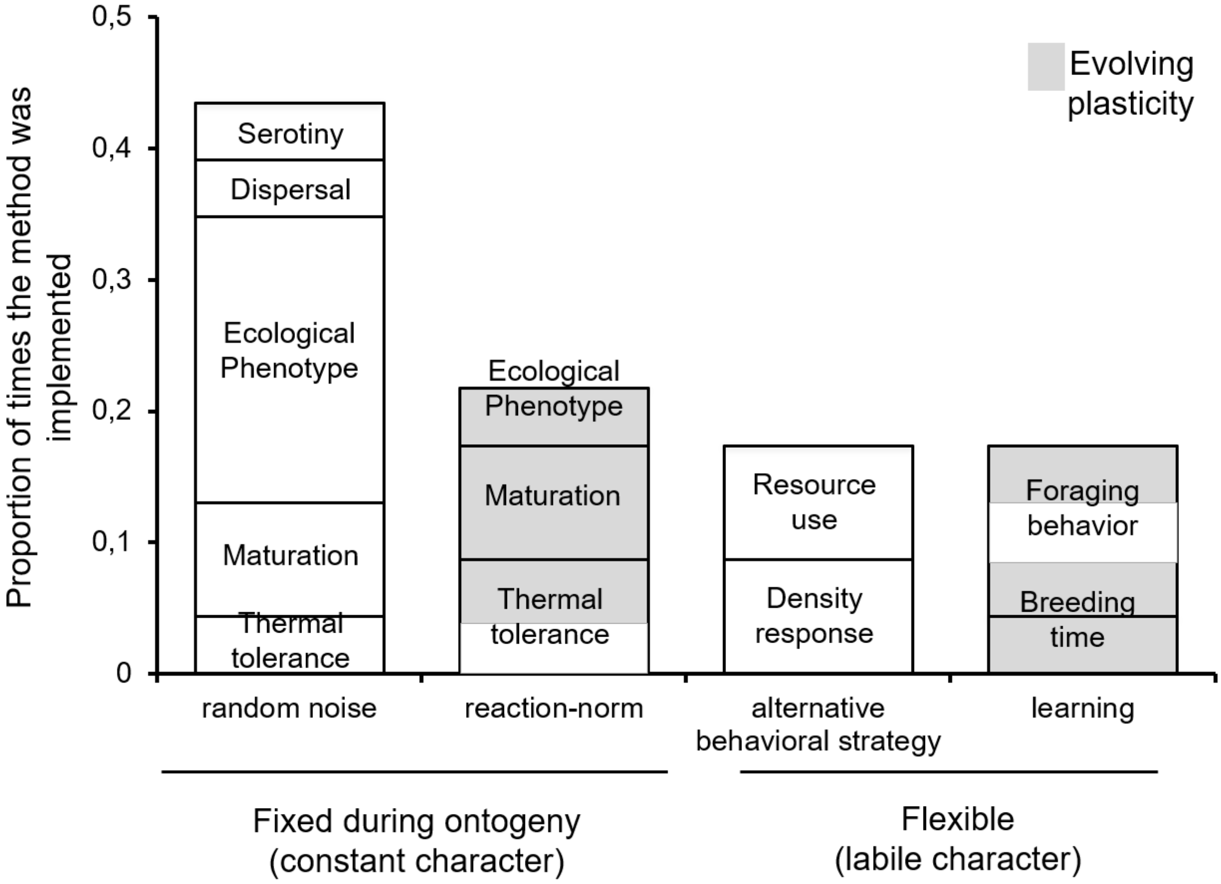


Fig. 2.2 Model implementation of plasticity. The model implementation was classified based on Lande (2014) as: fixed during ontogeny, when the resulting mature phenotype remained constant after a brief critical period of environmental influence early in life; or flexible, when the phenotype of an individual could fluctuate continuously and reversible throughout its life. Each implementation based the phenotypic plasticity on different environmental cues as indicated in the figure. Only in a few implementations, plasticity itself was an evolving trait (filled in grey).

2.5 Discussion

This review summarizes the state of the art of eco-evolutionary IBMs used to study organisms' responses to environmental change. IBMs simulate the basic entities upon which both ecological and evolutionary mechanisms act, which make them an attractive approach for eco-evolutionary research (DeAngelis and Mooij 2005; Dunlop et al. 2009). In particular, we focused on analyzing to what extent eco-evolutionary IBMs jointly account for the three potential adaptive responses of organisms facing environmental change: local genetic adaptation, plasticity, or dispersal. In addition, we compared prevailing methods found for the modelling of plasticity and its evolution. Most of the progress in eco-evolutionary IBMs in the last decades has been achieved for genetic adaptation to novel local environmental conditions. However, to date, no eco-evolutionary IBM addresses all three potential adaptive responses simultaneously. For example, although there is evidence for genetic variation in nature for plasticity (Pigliucci 2005), reviewed IBMs implementing adaptive phenotypic plasticity were rare. The most common method used for the implementation of plasticity was to assume a random noise in phenotypic characters, and for its evolution, reaction-norms and learning. These results highlight the evolution of plasticity as a knowledge gap and may motivate future studies for the understanding of how this feature adds to organisms' response to a changing environment.

According to our results on the state of the art, eco-evolutionary IBMs can be grouped into two distinct categories regarding the implementation of genetics: explicit or implicit (87.7% and 12.3% of the reviewed papers, respectively). In explicit genetics, loci and alleles are explicitly modeled, together with mechanisms for mutation and recombination. Often, in this method traits are under control of either one locus or multiple loci with additive effects. Traits under control of a single locus can lead to faster reduction in genetic variance for the trait at the population level, as compared to several loci (Bulmer 1971). On the other hand, assuming traits under control of several loci with additive effects can be more realistic when simulating quantitative traits (Lynch and Walsh 1998; Hill and Kirkpatrick 2010), although epistatic effects, while potentially common and relevant in reality, are neglected in these models. Explicit genetics is recommended if the focus is on the genetic mechanisms affecting the evolutionary process and the response of the population. For example, given that mutation rates have been empirically observed to differ among species and loci (Wolfe et al. 1989; Eyre-Walker and Keightley 2007), explicit genetics can be useful to understand how such differences in mutation rate affect the eco-evolutionary dynamics (Clark et al. 2011; Cobben et al. 2017). In contrast, in models with implicit genetics, mutation and recombination processes are implicit, based on the infinitesimal model of quantitative genetics (Lynch and Walsh 1998). One advantage of this method over the explicit one is the simplification of genetics, while still holding robust assumptions (Lynch and Walsh 1998; Hill and Kirkpatrick 2010). In this manner, the eco-evolutionary IBM could be focused more on the ecological module. Non-quantitative geneticist readers may think at first glance, that the implementation of implicit genetics, i.e., to inherit a midparent value, reminds of a common misconception in the early days of evolutionary thinking, i.e., blending inheritance (e.g., Fleeming 1867). However, such an implementation can be reconciled with the infinitesimal model of inheritance, i.e., a trait inherited by an infinite number of loci with only additive effects (i.e., without interaction and dominance). Indeed, implicit genetics has been successfully used for the understanding of the evolutionary potential of natural populations of fish under scenarios of moderate to rapid climate warming (Reed et al. 2011). Additionally, because of the relatively easy way to implement inheritance, implicit genetics could be an attractive approach when trying to address all three potential responses of organisms to environmental change simultaneously.

To date, according to our study, most eco-evolutionary IBMs are focused on genetic adaptation to local novel environmental conditions, and no single eco-evolutionary IBM addresses all three potential adaptive responses simultaneously. However, responses of populations of organisms to environmental change can depend on pre-existing abilities, for example already evolved reaction-norms due to past selection, as well as on the constraints of populations to evolve a given adaptive response. Empirical evidence and field observations has repeatedly proven that organisms can respond adaptively to environmental change (Johnston and Selander 1964; Boag and Grant 1981; Yoshida et al. 2003), and that phenotypic responses can appear and spread in a population by genetic or non-genetic mechanisms (Laland et al. 2015; Kronholm and Collins 2016). The strongest support for evolution occurring in ecological relevant time scales comes from the study of organisms with short generation time (Yoshida et al. 2003; Lohbeck et al. 2012). There is however an increasing awareness that rapid phenotypic responses can occur in many taxa, not only in those with short generation time. Generally, evolution in organisms with complex life cycles and large generation time is not well understood yet (Shefferson and Salguero-Gómez 2015). Future models need to consider the possibility for populations of organisms to develop adaptive responses to environmental change to understand for what life history characters and in what kind of environmental scenarios a particular response is preferred over the others. We consider, as in Dunlop et al. (2009), that the use of evolving traits – and their interplay – for the modelling of organisms' adaptive responses could help to identify the conditions promoting the recovery of declining populations (Evolutionary rescue – sensu Gonzalez et al. 2013). In this context, the more complex model is not necessarily the better one. Rather, it is about keeping model complexity simple enough, yet being able to exploit the advantage of IBMs for the modeling of adaptive systems. It is recommended that, once the three types of responses of organisms are jointly accounted for in the eco-evolutionary IBM, then the model can progressively start focusing on modeling evolutionary dynamics in the degree of plasticity (second tier challenge) and traits potentially causing range shift (third tier challenge).

Among the mentioned expected responses of organisms, phenotypic plasticity has received increasing attention due to its relatively immediate effect on the phenotype of individuals that are experiencing novel environmental conditions, which can lead to considerable ecological effects (Miner et al. 2005). The effect of phenotypic plasticity can occur within an individual's lifespan or between generations (transgenerational plasticity) (Galloway and Etterson 2007). In the presence of novel environmental conditions, plasticity may buffer potential fitness losses as compared to when there is no phenotypic adjustment (Hendry 2016). According to our results, the prevailing method in eco-evolutionary IBMs for the modeling of phenotypic plasticity is to assume a random noise in phenotypic characters. This method recognizes that there is an environmental effect on development, but it neglects any plastic adjustment in relation to the environmental variable of interest. Random noise can be considered as part of passive phenotypic plasticity (Coleman et al. 1994). On the other hand, plasticity can also be adaptive and therefore consistently correlated to specific environmental triggers (Schmitt et al. 2003). The ability for adaptive plasticity is shaped by evolution. Evidence has mounted that there is variation in nature for plastic responses within populations (Pigliucci 2005; Hendry 2016). Consequently, the degree of phenotypic plasticity can respond to selection (Nussey et al. 2005). Our results show that eco-evolutionary IBMs have just started to address the challenging task, as stated by Lande (2014), of considering phenotypic plasticity as an evolving trait for the understanding of organisms' responses to environmental change (12.3% of the reviewed papers). Most of the reviewed papers on evolving plasticity were focusing on fish species (Dunlop et al. 2007; Thériault et al. 2008; Nonaka et al. 2014). Therefore, the topic of adaptive phenotypic plasticity and its evolution is still underexplored in eco-evolutionary IBMs. According to our review, the most common method for modeling adaptive plasticity is the reaction norm approach, followed by learning and alternative behavioral strategies. From those, reaction norms and learning were sometimes evolving traits, addressing the evolution of phenotypic plasticity. In the former, the parameters describing the norm of reaction are assumed to be under genetic control, and therefore, heritable (Thériault et al. 2008). Here, a change in the intercept in the norm of reaction is analogous to direct genetic adaptation with no effect on the degree of plasticity, while additional parameters describing its shape (e.g., the slope of a linear reaction norm) dictate the degree of plasticity, which could also evolve. In learning, often the ability per se, or the learning strategy was assumed to evolve (Campos et al. 2008; Acerbi et al. 2012).

Another distinction among methods to model adaptive plasticity is related to whether the effect of phenotypic plasticity is fixed during ontogeny (constant character) or flexible (labile character), changing continuously and reversibly throughout an individual's life. Reaction norms commonly assume constant characters, while for the other methods the plastic characters can be labile. Moreover, the constant character is usually not directly linked to the environmental optimum, while the labile characters can be malleable as to track the optimum by direct feedback, as it occurs for learning. A question that remains is the understanding of costs and limits to either form of plasticity (Pigliucci 2005). "Costs result in a decrease in fitness even when an optimal phenotype is expressed" (Pigliucci 2005) and are usually associated with maintenance or energetic costs, sensing of environmental cues, and genetic costs when genes promoting plasticity are linked with genes that reduce fitness (DeWitt et al. 1998). In contrast, limits (or constraints) of plasticity occur when plasticity cannot produce a trait near to the optimum (DeWitt et al. 1998), and are related, for example, to information reliability, and lag time between the environmental change and the phenotypic response (see nine potential costs and limits of phenotypic plasticity in DeWitt et al. 1998). If there were neither costs nor limits, labile characters would always lead to the best phenotype in every environment (Lande 2014). However, though challenging to detect, costs of plasticity do occur in nature (Relyea 2002). Lande (2014) assumes labile characters to be costlier than constant ones, because they might need more energy to maintain the machinery that makes this kind of plasticity possible. However, more empirical evidence is needed to examine this assumption. So far, in IBMs few works have explicitly modelled costs to forms of plasticity (3.5% of the reviewed papers). On the other hand, IBMs often implicitly implemented limits of plasticity, and they depended on the form of plasticity and on the environmental scenario (Romero-Mujalli et al. 2017), being one example the random noise approach (Reed et al. 2011; Vincenzi 2014). Another example is when organisms able to learn failed to achieve the optimum phenotype when the social influence was strong, and the environmental change was slow (Romero-Mujalli et al. 2017).

In conclusion, future eco-evolutionary models should consider dispersal and plasticity, together with further relevant organismal characteristics, as evolving traits with their associated costs and benefits. Such an integrated approach will allow to investigate whether the type of evolved adaptive response differs among life history strategies of organisms, and whether this response varies for the same life history strategy depending on the characteristics of the environmental change. This could help to identify conditions promoting population persistence. In particular, future work needs to go beyond the random noise approach for plasticity, and start simulating plasticity as evolvable, passive or adaptive, constant or flexible, with its associated costs and limits according to what empirical evidence suggests.

2.6 Acknowledgements

We thank the research group of Plant Ecology and Nature Conservation of the University of Potsdam for their valuable comments on the manuscript. This work was funded by the University of Potsdam.

2.7 References

Acerbi A, Jacquet PO, Tennie C (2012) Behavioral constraints and the evolution of faithful social learning. Curr Zool 58:307–318. doi: 10.1093/czoolo/58.2.307

Aguilee R, Claessen D, Lambert A (2013) Adaptive radiation driven by the interplay of eco-evolutionary and landscape dynamics. Evolution 67:1291–1306. doi: 10.1111/evo.12008

Ayllón D, Railsback SF, Vincenzi S, Groeneveld J, Almodóvar A, Grimm V (2016) InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. Ecol Model 326:36–53. doi: 10.1016/j.ecolmodel.2015.07.026

Barfield M, Holt RD (2016) Evolutionary rescue in novel environments: towards improving predictability. Evol Ecol Res 17:771–786.

Barraquand F, Murrell DJ (2012) Intense or Spatially Heterogeneous Predation Can Select against Prey Dispersal. PLOS ONE 7:e28924. doi: 10.1371/journal.pone.0028924

Birand A, Vose A, Gavrilets S (2012) Patterns of Species Ranges, Speciation, and Extinction. Am Nat 179:1–21. doi: 10.1086/663202

Björklund M, Ranta E, Kaitala V, Bach LA, Lundberg P, Stenseth NC (2009) Quantitative Trait Evolution and Environmental Change. PLoS ONE 4:e4521. doi: 10.1371/journal.pone.0004521

Boag PT, Grant PR (1981) Intense Natural Selection in a Population of Darwin's Finches (Geospizinae) in the Galápagos. Science 214:82. doi: 10.1126/science.214.4516.82

Bocedi G, Palmer SCF, Pe'er G, Heikkinen RK, Matsinos YG, Watts K, Travis JMJ (2014) RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. Methods Ecol Evol 5:388–396. doi: 10.1111/2041-210X.12162

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. Trends Ecol Evol 26:183–192. doi: 10.1016/j.tree.2011.01.009

Bonte D, Hovestadt T, Poethke H-J (2010) Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. Oikos 119:560–566. doi: 10.1111/j.1600-0706.2009.17943.x

Boutin S, Lane JE (2014) Climate change and mammals: evolutionary versus plastic responses. Evol Appl 7:29–41. doi: 10.1111/eva.12121

Bridle JR, Polechová J, Kawata M, Butlin RK (2010) Why is adaptation prevented at ecological margins? New insights from individual-based simulations. Ecol Lett 13:485–494. doi: 10.1111/j.1461-0248.2010.01442.x

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. Trends Ecol Evol 23:453–460. doi: 10.1016/j.tree.2008.03.011

Bulmer MG (1971) The Effect of Selection on Genetic Variability. Am Nat 105:201–211. doi: 10.1086/282718

Bush A, Mokany K, Catullo R, Hoffmann A, Kellermann V, Sgrò C, McEvey S, Ferrier S, Coulson T (2016) Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecol Lett 19:1468–1478. doi: 10.1111/ele.12696

Campos D, Llebot JE, Méndez V (2008) Limited resources and evolutionary learning may help to understand the mistimed reproduction in birds caused by climate change. Theor Popul Biol 74:16–21. doi: 10.1016/j.tpb.2008.04.002

Chaianunporn T, Hovestadt T (2012) Concurrent evolution of random dispersal and habitat niche width in host-parasitoid systems. Ecol Model 247:241–250. doi: 10.1016/j.ecolmodel.2012.09.005

Charmantier A, Gienapp P (2014) Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. Evol Appl 7:15–28. doi: 10.1111/eva.12126

Chevin L-M, Lande R, Mace GM (2010) Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. PLoS Biol 8:e1000357. doi: 10.1371/journal.pbio.1000357

Clark JR, Daines SJ, Lenton TM, Watson AJ, Williams HTP (2011) Individual-based modelling of adaptation in marine microbial populations using genetically defined physiological parameters. Ecol Model 222:3823–3837. doi: 10.1016/j.ecolmodel.2011.10.001

Cobben MMP, Mitesser O, Kubisch A (2017) Evolving mutation rate advances the invasion speed of a sexual species. BMC Evol Biol 17:150. doi: 10.1186/s12862-017-0998-8

Coleman JS, McConnaughay KDM, Ackerly DD (1994) Interpreting phenotypic variation in plants. Trends Ecol Evol 9:187–191. doi: 10.1016/0169-5347(94)90087-6

Collins S, Rost B, Rynearson TA (2014) Evolutionary potential of marine phytoplankton under ocean acidification. Evol Appl 7:140–155. doi: 10.1111/eva.12120

Crone EE, Ellis MM, Morris WF, Stanley A, Bell T, Bierzychudek P, Ehrlén J, Kaye TN, Knight TM, Lesica P, Oostermeijer G, Quintana-Ascencio PF, Ticktin T, Valverde T, Williams JL, Doak DF, Ganesan R, Mceachern K, Thorpe AS, Menges ES (2013) Ability of Matrix Models to Explain the Past and Predict the Future of Plant Populations. Conserv Biol 27:968–978. doi: 10.1111/cobi.12049

Crozier LG, Hutchings JA (2014) Plastic and evolutionary responses to climate change in fish. Evol Appl 7:68–87. doi: 10.1111/eva.12135

DeAngelis DL, Grimm V (2014) Individual-based models in ecology after four decades. F1000Prime Rep 6:39. doi: 10.12703/P6-39

DeAngelis DL, Mooij WM (2005) Individual-Based Modeling of Ecological and Evolutionary Processes. Annu Rev Ecol Evol Syst 36:147–168. doi: 10.1146/annurev.ecolsys.36.102003.152644

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. Trends Ecol Evol 13:77–81. doi: 10.1016/S0169-5347(97)01274-3

Downing K (1998) Using evolutionary computational techniques in environmental modelling. Environ Model Softw 13:519–528. doi: 10.1016/S1364-8152(98)00050-4

Dunlop ES, Heino M, Dieckmann U (2009) Eco-genetic modeling of contemporary life-history evolution. Ecol Appl 19:1815–1834. doi: 10.1890/08-1404.1

Dunlop ES, Shuter BJ, Dieckmann U (2007) Demographic and Evolutionary Consequences of Selective Mortality: Predictions from an Eco-Genetic Model for Smallmouth Bass. Trans Am Fish Soc 136:749–765. doi: 10.1577/T06-126.1

Dytham C (2009) Evolved dispersal strategies at range margins. Proc R Soc B 276:1407. doi: 10.1098/rspb.2008.1535

Dytham C, Travis JMJ, Mustin K, Benton TG (2014) Changes in species' distributions during and after environmental change: which eco-evolutionary processes matter more? Ecography 37:1210–1217. doi: 10.1111/ecog.01194

Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu Rev Ecol Evol Syst 40:677–697. doi: 10.1146/annurev.ecolsys.110308.120159

Eyre-Walker A, Keightley PD (2007) The distribution of fitness effects of new mutations. Nat Rev Genet 8:610–618. doi: 10.1038/nrg2146

Fleeming J (1867) (Review of) "The origin of species." North Br Rev 46:277–318.

Franks SJ, Weber JJ, Aitken SN (2014) Evolutionary and plastic responses to climate change in terrestrial plant populations. Evol Appl 7:123–139. doi: 10.1111/eva.12112

Fronhofer EA, Kubisch A, Hilker FM, Hovestadt T, Poethke HJ (2012) Why are metapopulations so rare? Ecology 93:1967–1978. doi: 10.1890/11-1814.1

Fronhofer EA, Nitsche N, Altermatt F (2017) Information use shapes the dynamics of range expansions into environmental gradients. Glob Ecol Biogeogr 26:400–411. doi: 10.1111/geb.12547

Fussmann GF, Ellner SP, Hairston NG (2003) Evolution as a critical component of plankton dynamics. Proc R Soc B 270:1015–1022. doi: 10.1098/rspb.2003.2335

Galloway LF, Etterson JR (2007) Transgenerational Plasticity Is Adaptive in the Wild. Science 318:1134. doi: 10.1126/science.1148766

Gilbert KJ, Whitlock MC (2017) The genetics of adaptation to discrete heterogeneous environments: frequent mutation or large-effect alleles can allow range expansion. J Evol Biol 30:591–602. doi: 10.1111/jeb.13029

Gilman RT, Behm JE (2011) Hybridization, species collapse, and species reemergence after disturbance to premating mechanisms of reproductive isolation. Evolution 65:2592–2605. doi: 10.1111/j.1558-5646.2011.01320.x

Golestani A, Gras R, Cristescu M (2012) Speciation with gene flow in a heterogeneous virtual world: can physical obstacles accelerate speciation? Proc R Soc B 279:3055–3064. doi: 10.1098/rspb.2012.0466

Gonzalez A, Ronce O, Ferriere R, Hochberg ME (2013) Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. Philos Trans R Soc B Biol Sci 368:20120404. doi: 10.1098/rstb.2012.0404

Green DM (2009) Coevolution of dispersal in a parasitoid–host system. Popul Ecol 51:253–260. doi: 10.1007/s10144-008-0131-3

Griebeler EM, Caprano T, Böhning-Gaese K (2010) Evolution of avian clutch size along latitudinal gradients: do seasonality, nest predation or breeding season length matter? J Evol Biol 23:888–901. doi: 10.1111/j.1420-9101.2010.01958.x

Guttal V, Couzin ID (2010) Social interactions, information use, and the evolution of collective migration. Proc Natl Acad Sci 107:16172–16177. doi: 10.1073/pnas.1006874107

Haller BC, Mazzucco R, Dieckmann U (2013) Evolutionary Branching in Complex Landscapes. Am Nat 182:E127–E141. doi: 10.1086/671907

Hanski I, Heino M (2003) Metapopulation-level adaptation of insect host plant preference and extinction–colonization dynamics in heterogeneous landscapes. Theor Popul Biol 64:281–290. doi: 10.1016/S0040-5809(03)00093-5

Haythorne S, Skabar A (2013) An improved pattern-guided evolution approach for the development of adaptive individual-based ecological models. Ecol Model 252:72–82. doi: 10.1016/j.ecolmodel.2012.09.002

Heino M, Hanski I (2001) Evolution of Migration Rate in a Spatially Realistic Metapopulation Model. Am Nat 157:495–511. doi: 10.1086/319927

Hendry AP (2016) Key Questions on the Role of Phenotypic Plasticity in Eco-Evolutionary Dynamics. J Hered 107:25–41. doi: 10.1093/jhered/esv060

Hill WG, Kirkpatrick M (2010) What Animal Breeding Has Taught Us about Evolution. Annu Rev Ecol Evol Syst 41:1–19. doi: 10.1146/annurev-ecolsys-102209-144728

Holt RD, Barfield M (2011) Theoretical Perspectives on the Statics and Dynamics of Species' Borders in Patchy Environments. Am Nat 178:S6–S25. doi: 10.1086/661784

Jager HI (2001) Individual variation in life history characteristics can influence extinction risk. Ecol Model 144:61–76. doi: 10.1016/S0304-3800(01)00362-3

Jeltsch F, Moloney KA, Schurr FM, Köchy M, Schwager M (2008) The state of plant population modelling in light of environmental change. Perspect Plant Ecol Evol Syst 9:171–189. doi: 10.1016/j.ppees.2007.11.004

Jeltsch F, Moloney KA, Schwager M, Körner K, Blaum N (2011) Consequences of correlations between habitat modifications and negative impact of climate change for regional species survival. Agric Ecosyst Environ 145:49–58. doi: 10.1016/j.agee.2010.12.019

Johnston RF, Selander RK (1964) House Sparrows: Rapid Evolution of Races in North America. Science 144:548. doi: 10.1126/science.144.3618.548

Katsnelson E, Motro U, Feldman MW, Lotem A (2012) Evolution of learned strategy choice in a frequency-dependent game. Proc R Soc B 279:1176–1184. doi: 10.1098/rspb.2011.1734

Kearney M, Porter WP, Williams C, Ritchie S, Hoffmann AA (2009) Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito Aedes aegypti in Australia. Funct Ecol 23:528–538. doi: 10.1111/j.1365-2435.2008.01538.x

Kronholm I, Collins S (2016) Epigenetic mutations can both help and hinder adaptive evolution. Mol Ecol 25:1856–1868. doi: 10.1111/mec.13296

Kubisch A, Hovestadt T, Poethke H-J (2010) On the elasticity of range limits during periods of expansion. Ecology 91:3094–3099. doi: 10.1890/09-2022.1

Laland KN, Odling-Smee FJ, Feldman MW (1999) Evolutionary consequences of niche construction and their implications for ecology. Proc Natl Acad Sci 96:10242–10247. doi: 10.1073/pnas.96.18.10242

Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. Proc R Soc B 282: doi: 10.1098/rspb.2015.1019

Lande R (2014) Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. J Evol Biol 27:866–875. doi: 10.1111/jeb.12360

Litchman E, Klausmeier CA (2008) Trait-based community ecology of phytoplankton. Annu Rev Ecol Evol Syst 39:615–639. doi: 10.1146/annurev.ecolsys.39.110707.173549

Lohbeck KT, Riebesell U, Reusch TBH (2012) Adaptive evolution of a key phytoplankton species to ocean acidification. Nat Geosci 5:346–351. doi: 10.1038/ngeo1441

Lynch M, Walsh B (1998) Genetics and Analysis of Quantitative Traits. Sinauer, Sunderland, MA

Merico A, Brandt G, Smith SL, Oliver M (2014) Sustaining diversity in trait-based models of phytoplankton communities. Front Ecol Evol 2:59. doi: 10.3389/fevo.2014.00059

Merow C, Dahlgren JP, Metcalf CJ, Childs DZ, Evans ME, Jongejans E, Record S, Rees M, Salguero-Gómez R, McMahon SM, Ramula S (2014) Advancing population ecology with integral projection models: a practical guide. Methods Ecol Evol 5:99–110. doi: 10.1111/2041-210X.12146

Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences of phenotypic plasticity. Trends Ecol Evol 20:685–692. doi: 10.1016/j.tree.2005.08.002

Mokany K, Ferrier S, Connolly SR, Dunstan PK, Fulton EA, Harfoot MB, Harwood TD, Richardson AJ, Roxburgh SH, Scharlemann JP, Tittensor DP, Westcott DA, Wintle BA (2015) Integrating modelling of biodiversity composition and ecosystem function. Oikos 125:10–19. doi: 10.1111/oik.02792

Moustakas A, Evans MR (2013) Integrating Evolution into Ecological Modelling: Accommodating Phenotypic Changes in Agent Based Models. PLOS ONE 8:e71125. doi: 10.1371/journal.pone.0071125

Moya-Laraño J, Verdeny-Vilalta O, Rowntree J, Melguizo-Ruiz N, Montserrat M, Laiolo P (2012) Chapter 1 - Climate Change and Eco-Evolutionary Dynamics in Food Webs. In: Guy Woodward UJ and EJO (ed) Advances in Ecological Research. Academic Press, pp 1–80

Nonaka E, Brännström Å, Svanbäck R (2014) Assortative mating can limit the evolution of phenotypic plasticity. Evol Ecol 28:1057–1074. doi: 10.1007/s10682-014-9728-5

North A, Cornell S, Ovaskainen O (2011) Evolutionary responses of dispersal distance to landscape structure and habitat loss. Evolution 65:1739–1751. doi: 10.1111/j.1558-5646.2011.01254.x

Nussey DH, Postma E, Gienapp P, Visser ME (2005) Selection on Heritable Phenotypic Plasticity in a Wild Bird Population. Science 310:304. doi: 10.1126/science.1117004

Oddou-Muratorio S, Davi H (2014) Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. Evol Appl 7:453–467. doi: 10.1111/eva.12143

Phillips BL (2012) Range shift promotes the formation of stable range edges. J Biogeogr 39:153–161. doi: 10.1111/j.1365-2699.2011.02597.x

Picó FX, Quintana-Ascencio PF, Mildén M, Ehrlén J, Pfingsten I (2009) Modelling the effects of genetics and habitat on the demography of a grassland herb. Basic Appl Ecol 10:122–130. doi: 10.1016/j.baae.2008.02.006

Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? Trends Ecol Evol 20:481–486. doi: 10.1016/j.tree.2005.06.001

Poethke HJ, Dytham C, Hovestadt T (2011) A Metapopulation Paradox: Partial Improvement of Habitat May Reduce Metapopulation Persistence. Am Nat 177:792–799. doi: 10.1086/659995

Rebaudo F, Le Rouzic A, Dupas S, Silvain J-F, Harry M, Dangles O (2013) SimAdapt: an individual-based genetic model for simulating landscape management impacts on populations. Methods Ecol Evol 4:595–600. doi: 10.1111/2041-210X.12041

Reed TE, Schindler DE, Hague MJ, Patterson DA, Meir E, Waples RS, Hinch SG (2011) Time to Evolve? Potential Evolutionary Responses of Fraser River Sockeye Salmon to Climate Change and Effects on Persistence. PLOS ONE 6:e20380. doi: 10.1371/journal.pone.0020380

Relyea RA (2002) Costs of Phenotypic Plasticity. Am Nat 159:272–282. doi: 10.1086/338540

Romero-Mujalli D, Cappelletto J, Herrera EA, Tárano Z (2017) The effect of social learning in a small population facing environmental change: an agent-based simulation. J Ethol 35:61–73. doi: 10.1007/s10164-016-0490-8

Sadedin S, Hollander J, Panova M, Johannesson K, Gavrilets S (2009) Case studies and mathematical models of ecological speciation. 3: Ecotype formation in a Swedish snail. Mol Ecol 18:4006–4023. doi: 10.1111/j.1365-294X.2009.04320.x

Schilthuizen M, Kellermann V (2014) Contemporary climate change and terrestrial invertebrates: evolutionary versus plastic changes. Evol Appl 7:56–67. doi: 10.1111/eva.12116

Schmitt J, Stinchcombe JR, Heschel MS, Huber H (2003) The Adaptive Evolution of Plasticity: Phytochrome-Mediated Shade Avoidance Responses1. Integr Comp Biol 43:459–469. doi: 10.1093/icb/43.3.459

Schweitzer JA, Juric I, van de Voorde TFJ, Clay K, van der Putten WH, Bailey JK (2014) Are there evolutionary consequences of plant–soil feedbacks along soil gradients? Funct Ecol 28:55–64. doi: 10.1111/1365-2435.12201

Shefferson RP, Salguero-Gómez R (2015) Eco-evolutionary dynamics in plants: interactive processes at overlapping time-scales and their implications. J Ecol 103:789–797. doi: 10.1111/1365-2745.12432

Stillman RA, Railsback SF, Giske J, Berger U, Grimm V (2015) Making Predictions in a Changing World: The Benefits of Individual-Based Ecology. Bioscience 65:140–150. doi: 10.1093/biosci/biu192

Stoks R, Geerts AN, De Meester L (2014) Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. Evol Appl 7:42–55. doi: 10.1111/eva.12108

Thériault V, Dunlop ES, Dieckmann U, Bernatchez L, Dodson JJ (2008) The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. Evol Appl 1:409–423. doi: 10.1111/j.1752-4571.2008.00022.x

Travis JMJ, Mustin K, Bartoń KA, Benton TG, Clobert J, Delgado MM, Dytham C, Hovestadt T, Palmer SCF, Van Dyck H, Bonte D (2012) Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods Ecol Evol 3:628–641. doi: 10.1111/j.2041-210X.2012.00193.x

Travis JMJ, Smith HS, Ranwala SMW (2010) Towards a mechanistic understanding of dispersal evolution in plants: conservation implications. Divers Distrib 16:690–702. doi: 10.1111/j.1472-4642.2010.00674.x

Urban MC, De Meester L (2009) Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. Proc R Soc B 276:4129. doi: 10.1098/rspb.2009.1382

Urban MC, Richardson JL, Freidenfelds NA (2014) Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evol Appl 7:88–103. doi: 10.1111/eva.12114

van der Post DJ, Semmann D (2011) Local Orientation and the Evolution of Foraging: Changes in Decision Making Can Eliminate Evolutionary Trade-offs. PLOS Comput Biol 7:e1002186. doi: 10.1371/journal.pcbi.1002186

Vincenzi S (2014) Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. J R Soc Interface 11:20140441. doi: 10.1098/rsif.2014.0441

Vincenzi S, Crivelli AJ, Satterthwaite WH, Mangel M (2014) Eco-evolutionary dynamics induced by massive mortality events. J Fish Biol 85:8–30. doi: 10.1111/jfb.12382

Vincenzi S, Piotti A (2014) Evolution of serotiny in maritime pine (Pinus pinaster) in the light of increasing frequency of fires. Plant Ecol 215:689–701. doi: 10.1007/s11258-014-0342-y

Wang H-Y, Höök TO (2009) Eco-genetic model to explore fishing-induced ecological and evolutionary effects on growth and maturation schedules. Evol Appl 2:438–455. doi: 10.1111/j.1752-4571.2009.00088.x

West-Eberhard MJ (2003) Developmental Plasticity and Evolution. Oxford University Press

Wiens JJ (2016) Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. PLOS Biol 14:e2001104. doi: 10.1371/journal.pbio.2001104

Wolfe KH, Sharp PM, Li W-H (1989) Mutation rates differ among regions of the mammalian genome. Nature 337:283–285. doi: 10.1038/337283a0

Yoshida T, Jones LE, Ellner SP, Fussmann GF, Hairston NG (2003) Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424:303–306. doi: 10.1038/nature01767

Zheng C, Ovaskainen O, Hanski I (2009) Modelling single nucleotide effects in phosphoglucose isomerase on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. Philos Trans R Soc B Biol Sci 364:1519. doi: 10.1098/rstb.2009.0005

Chapter 3

Elevated mutation rates are unlikely to evolve in sexual species, not even under rapid environmental change

CHAPTER 3

Elevated mutation rates are unlikely to evolve in sexual species, not even under rapid environmental change

Daniel Romero-Mujalli[1,2], Florian Jeltsch[2,3], and Ralph Tiedemann[1]

This Chapter is submitted to *BMC Evolutionary Biology Journal*

Manuscript Number:	EVOB-D-18-00374R2
Full Title:	Elevated mutation rates are unlikely to evolve to elevated values in sexual species, not even under rapid environmental change
Article Type:	Research article
Section/Category:	Theories and Models

[1] University of Potsdam, Evolutionary Biology/Systematic Zoology, Karl-Liebknecht-Strasse 24-25, 14476 Potsdam, Germany

[2] University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlenberg 3, 14476 Potsdam, Germany

[3] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany

3.1 Abstract

Organisms are expected to respond to changing environmental conditions through local adaptation, range shift or local extinction. The process of local adaptation can occur by genetic changes or phenotypic plasticity, and becomes especially relevant when dispersal abilities or possibilities are somehow constrained. For genetic changes to occur, mutations are the ultimate source of variation and the mutation rate in terms of a mutator locus can be subject to evolutionary change. Recent findings suggest that the evolution of the mutation rate in a sexual species can advance invasion speed and promote adaptation to novel environmental conditions. Following this idea, this work uses and individual-based model approach to investigate if the mutation rate can also evolve in a sexual species experiencing different conditions of directional climate change, under different scenarios of probability of recombination and of beneficial mutations. The results suggest that the mutation rate in a sexual species experiencing directional climate change scenarios can evolve and reach relatively high values mainly under conditions of complete linkage of the mutator locus and the adaptation locus. In contrast, when they are unlinked, the mutation rate can slightly increase only under scenarios where at least 50% of arising mutations are beneficial and the rate of environmental change is relatively high. Given that 50% beneficial mutations may be an unrealistic assumption, and that recombination is ubiquitous in sexual species, the evolution of an elevated mutation rate in a sexual species experiencing directional climate change might be rather unlikely. Furthermore, when the percentage of beneficial mutations and the population size are small, sexual species (especially multicellular ones) producing few offspring may be expected to react to changing environments not by adaptive genetic change, but mainly through plasticity. Without the ability for a plastic response, such species may become – at least locally – extinct.

Keywords

Individual-based models; mutation rate; mutator locus; directional climate change; recombination; beneficial mutations, sexual species

3.2 Introduction

Local adaptation to changing environmental conditions, such as directional climate change, becomes of high importance for organisms with limited dispersal abilities, or when physical barriers preventing dispersal are present.

In such scenarios, organisms can adapt by genetic changes and / or phenotypic plasticity. For genetic changes to occur, mutations are the ultimate source of novel variation, and it is generally assumed that a mutation is a rare event (1). Consequently, individual-based models of explicit genetics typically assume small and constant (*i.e.*, non-evolving) mutation rates (2–4). According to evidence, only few mutations are adaptive; many deleterious; and some are neutral (5). There is however genetic variation in DNA repair and replication processes (6–9), affecting the probability of a mutation to occur. Genetic loci affecting the origin of new variation (*i.e.*, the mutation rate) have been termed "mutator" loci. They may be subject to selection, and selective forces may depend on the environmental context or scenario.

Previous work investigating the evolution of the mutation rate has found that the fate of mutator alleles may differ for sexual and asexual organisms (10,11). In asexual organisms mutator alleles are associated with the mutations they caused, thus mutator alleles leading to an increase of the mutation rate can increase in frequency by hitchhiking with beneficial mutations at other loci (12). In contrast, in sexual organisms given that recombination breaks linkage disequilibrium, the mutator allele will be separated soon from a beneficial mutation it has caused and will not hitchhike to high frequency (10). Consequently, the evolution of mutation rate for a sexual organism is rather unlikely, and the mutation rate is then expected to stay close to a minimum achievable, limited either, by the costs of replication fidelity or by the drift limit (13,14).

Contrary to previous authors, a recent simulation study suggests that the mutation rate can evolve to relatively high values also in sexual species and this can advance invasion speed and promote adaptation to novel environmental conditions along an environmental gradient (15). The proposed mechanism is induced linkage disequilibrium between the dispersal locus and the mutator locus (both were evolving traits) that arise from spatial sorting and iterated founder event (15). The same authors also found that these results still held under assumptions of 90% of the mutations being lethal.

The present work uses an individual-based modeling approach focused on local adaptation to test the evolution of the mutation rate in a population of a sexual species experiencing directional climate change, under different scenarios of linkage disequilibrium (unlinked to complete linkage). The aim was to investigate, following the findings of Cobben et al (15), whether directional climate change scenarios can also lead to the evolution of an elevated mutation rate in a sexual species. This work employs an alternative method for the simulation of beneficial mutations, *i.e.*, implementing a distribution of mutation effects inspired by the concept of slightly deleterious mutations (16,17). Furthermore, different scenarios of stochasticity or noise color were explored to test whether the mutation rate could vary among organisms experiencing different habitats.

3.3 Methods

In order to investigate the evolution of the mutation rate under directional climate change scenarios, we designed a spatially implicit individual-based model (IBM) of a panmictic diploid population of a sexual species with non-overlapping generations experiencing directional climate change (a trend of the mean climatic variable such as temperature). Our model is based on two previous IBMs: Björklund et al. (18) for the simulation of environmental scenarios (including noise color) and the density dependence effect on fecundity; and Cobben et al. (15), for the simulation of explicit genetics on the inheritance of mutator and adaptation loci. The population was assumed to be geographically isolated, thus no migration was possible, such that the focus was on local adaptation. The mutation rate could evolve, and different scenarios of linkage disequilibrium and beneficial mutations were considered.

3.3.1 Environment

The environment was stochastic and defined an optimum mean phenotype θ_t that moved at constant speed per generation. This environmental scenario has been considered best suit to investigate the effect of climate change (19,20). Thus, $\theta_t = \theta_0 + \eta t$ impose the directional climate trend, where $\theta_0 = 0$ was the initial environmental optimum (when $t = 0$) and η, the rate of environmental change. The parameter η was changed to simulate different scenarios of environmental change (*e.g.*, no change, slow, medium, rapid change).

Environmental stochasticity or noise color was implemented as follows: The parameter $\theta^*_t = \theta_t + \phi_t$, was the realized environmental state with noise $\phi_t = \alpha\phi_{t-1} + \beta\xi_t$. The autocorrelation coefficient α indicated the level of environmental correlation and therefore the noise color: $-1 < \alpha < 0$, blue noise; $\alpha = 0$, white noise, and $0 < \alpha < 1$, red noise. Three scenarios of α were considered, based on Björklund et al. (18): blue noise ($\alpha = -0.7$); white noise ($\alpha = 0$), and red noise ($\alpha = 0.7$). The parameter β determined the environmental variance, according to $\beta = \sigma\sqrt{1 - \alpha^2}$, as in (21), where $\sigma^2 = 1$ was the environmental variance. The parameter ξ_t was a random value, normally distributed with zero mean and unity of variance.

3.3.2 Population dynamics

Individuals in the population were characterized by the following traits: sex, stage (whether adult or juvenile), phenotype zi, determined by the alleles at the adaptation locus, and a mutator locus whose alleles determine the genetic mutation rate. The phenotype and the mutator locus were considered evolving traits for the model. At the beginning of each simulation run, the population composed of 1000 individuals, at carrying capacity K, was assumed to be locally adapted. Therefore the alleles coding for the phenotype were initialize randomly from a normal distribution centered in θ_0 and variance $V = VG / 2L$, where VG is the initial genetic variance present in the population, and L the number of loci which was set to 1 for all runs in this study. The phenotype z of individual i was determined by additive effects of alleles at the adaptation locus. As in Cobben et al. (15) the mutation rate was given by $\mu = 10^{-exp}$, where *exp* = $(l_{m,1} + l_{m,2}) / 2$. The alleles at the mutator locus $l_{m,1}$ and $l_{m,2}$ were initialized randomly according to a discrete uniform distribution in range *[2; 4]*. Therefore, the model's initial conditions already incorporated intraspecific variation in the mutation rate between individuals in the population (initial mean mutation rate of 10^{-3}). Assuming initial intraspecific variation in the mutation rate facilitates its evolutionary dynamic and reduces an otherwise relatively high extinction risk during early simulation time.

3.3.3 Degree of local adaptation

Each individual was tested on its ability for local adaptation given by the match of its phenotype *zi* to the current environmental optimum θ_t. Stabilizing selection was assumed according to:

$$wi = e^{\frac{-(zi - \theta t)^2}{2\gamma^2}}$$

The variable *wi* indicates the degree of local adaptation of individual *i*, and *γ*, the strength of selection, affected the width of the fitness function, and was set to 2.2. This means that individuals having a phenotype departing from the optimum in *1SD* phenotypic units will have a fitness of 90% (relative to the maximum fitness) which would be moderate selection according to (18).

3.3.4 Fecundity

The mating system was random mating, where females mated only once and males could repeat mating (lottery polygyny). The fecundity *λ* of the reproductive couple was the sum of the scaled degree of local adaptation values *w'i* after considering density dependence effects, as in Björklund et al (18):

$$w'i = wie^{(1-\frac{N}{K})}$$

where *N* is the population size and *K*, the carrying capacity. Each couple (partners *i,j*) produced a number of offspring randomly drawn from a Poisson distribution with expectancy $\lambda = w'i + w'j$

3.3.5 Inheritance

Two scenarios of recombination were considered: unlinked and complete linkage (Table 3.1). During the process of inheritance, allele values for each locus (adaptation locus and mutator locus) of the inherited haplotype were picked randomly from the corresponding parental locus (unlinked scenario). In complete linkage scenario, alleles at the mutator locus were linked and migrated together with the corresponding alleles at the adaptation locus. For comparison, we also implemented an intermediate linkage ($pR = 0.5$). Then, mutations took place with probability μ determined by the alleles at the mutator locus as explained above. In case that a mutation occurred, its effect for the adaptation locus was randomly drawn from a normal distribution with zero mean and variance equals to the variance of the distribution of fitness effect size of mutations, which was an input parameter (20). The assumption of a Gaussian distribution is consistent with analysis of mutation effects (22,23). In the model, the mean x of the distribution of mutation effect size could change according to the scenario of percentage of beneficial mutations (input parameter, Table 3.1). This applied for the adaptation locus only. This approach granted that beneficial mutations – mutations that pushed the trait in the direction of θ_t – actually occurred at different probabilities as shown in the distribution of mutations fitness effect size (Figure 3.1). This can be important since under scenarios of directional selection the common assumption in individual-based models of explicit genetics of symmetric distribution of beneficial and deleterious mutations can overestimate the amount of arising beneficial mutations (*e.g.*, 12,17). In fact, the shifted distributions approximates the mutational effects according to the model of slightly deleterious mutations (16,17). On the other hand, when a mutation occurred at the mutator locus, its effect consisted in adding a value randomly drawn from [-1, 0, 1] to the mutated allele.

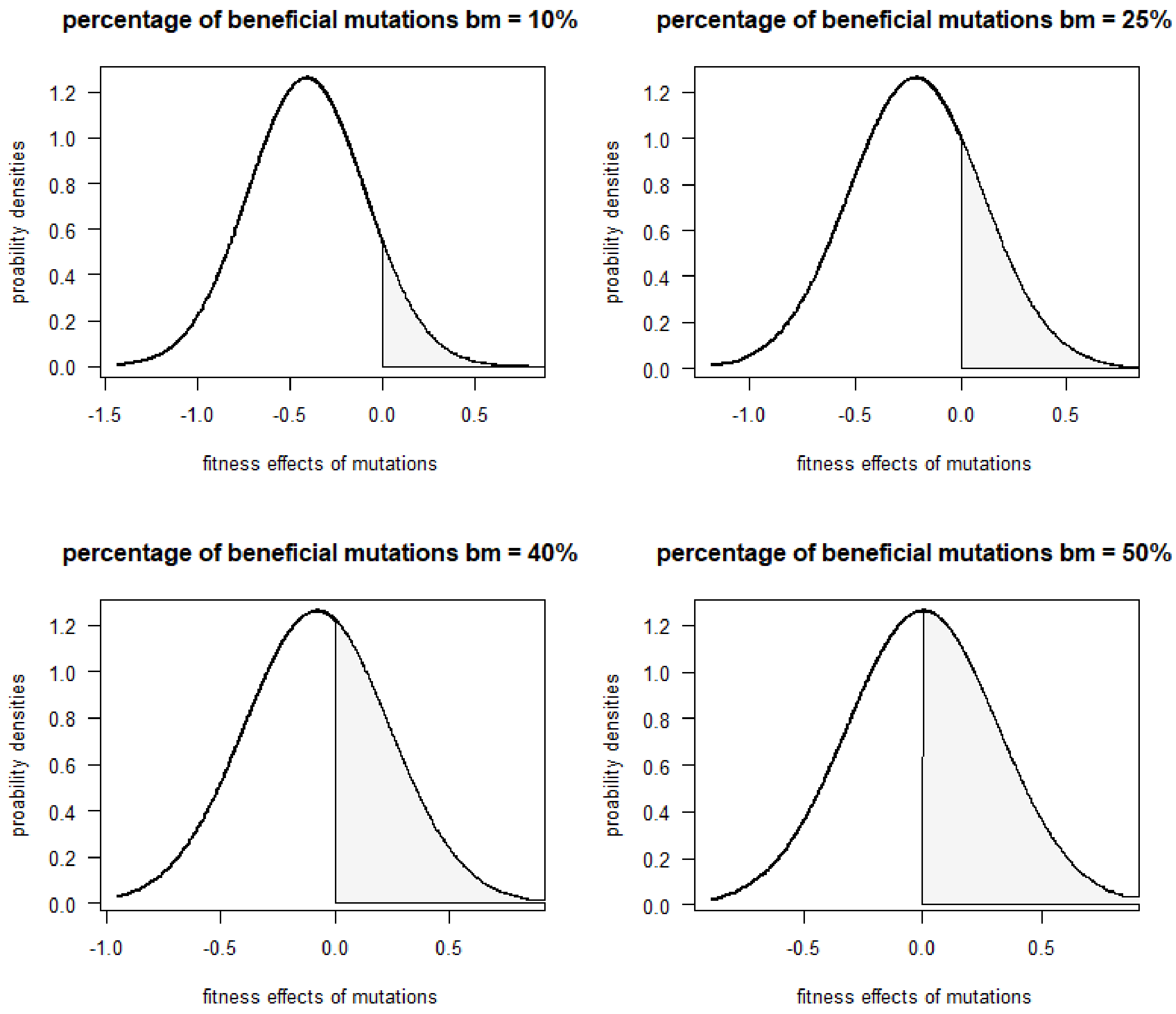


Fig. 3.1 Distribution of fitness effects of mutations according to different scenarios of percentage of beneficial mutations *bm*. Beneficial mutations are shown in light grey color. Variance of the distribution *MV = 0.1*

After the process of inheritance, all adults died, and newborns took over the population (non-overlapping generations).

3.3.6 Method for beneficial mutations

The mean x of the distribution of mutation effect size was given by $x = \varepsilon - y\sqrt{MV}$, where $\varepsilon = 0$ was the Z-score cutting value between deleterious and beneficial mutations. The parameter MV was the variance of the distribution, and y was given by the quantile function of the normal distribution with probability $p = 1 - q$. The parameter q was the desired proportion of beneficial mutation (e.g., 0.25 for 25% scenario of beneficial mutations).

3.3.7 Simulation experiments

To study the evolution of the mutation rate, different scenarios of rate of environmental change, probability of recombination, and percentage of beneficial mutations were implemented (Table 3.1). The environmental condition $r = 0$ (no directional climate change) was performed only for the scenario of $bm = 50\%$ and acted as a control. The additional scenarios of bm were performed for conditions of directional climate change ($r > 0$). Simulation experiments consisted of 200 replicates, lasting for 300 generations each: 100 generations of stable environment followed by 200 generations of treatment of directional climate change. The sequence of operations in the model were: update of the environmental optimum, degree of local adaptation, reproduction, mortality of adults, and update of phenotype of the new generation before repeating the loop. If extinctions occurred, the data was not used for the analysis.

The visualization of the data was done in r project v3.4.2 and the model was programmed in Netlogo v6.0.2.

Table 3.1 Parameters values and description (values in parentheses were implemented to evaluate the robustness of outcomes).

Parameter	Value	Description
K	1000	Carrying capacity
γ	2.2 (3.2)	Strength of selection
σ^2	1	Variance of the stochastic environment
θ_0	0	Initial environmental optimum
η	0, 0.01, 0.02, 0.03, 0.04	Rate of environmental change
z	evolving trait	Ecological phenotype
VG	0.2	Initial genetic variance present in the population
L	Number of loci per evolving trait	1
μ	evolving trait, range [0; 1]	Mutation rate
MV	0.2	Variance of the distribution of mutations fitness effect size
bm	10, 25, 40, 50	Percentage (%) of beneficial mutations
pR	0 (unlinked), (0.5), 1 (complete linkage),	Probability of recombination
t	300	Time limit per simulation, in generations. The last 200 generations were exposed to the treatment of directional climate change

3.4 Results

In our simulations, the mutation rate followed different evolutionary trajectories, relative to the percentage of beneficial mutation *bm* and the probability of recombination *pR*: Overall, the evolved mutation rate reached higher values when increasing the percentage of beneficial mutations *bm*, and this was independent of scenarios of probability of recombination *pR* and rate of environmental change (Figure 3.2, Figure 3A.3, Appendix 3A). The mutation rate evolved to relatively high values mainly under scenarios of complete linkage ($pR = 1$), relatively rapid directional climate change, and 25% or higher percentage of beneficial mutations (Figure 3.2). Under the unlinked recombination scenario ($pR = 0$), the mutation rate evolved to relatively high values only if the rate of environmental change was fast ($\eta = 0.04$) and the percentage of beneficial mutations was high (50%; Figure 3.2). An intermediate recombination rate ($pR = 0.5$) yielded intermediate results (Figure 3A.1 Appendix 3A).

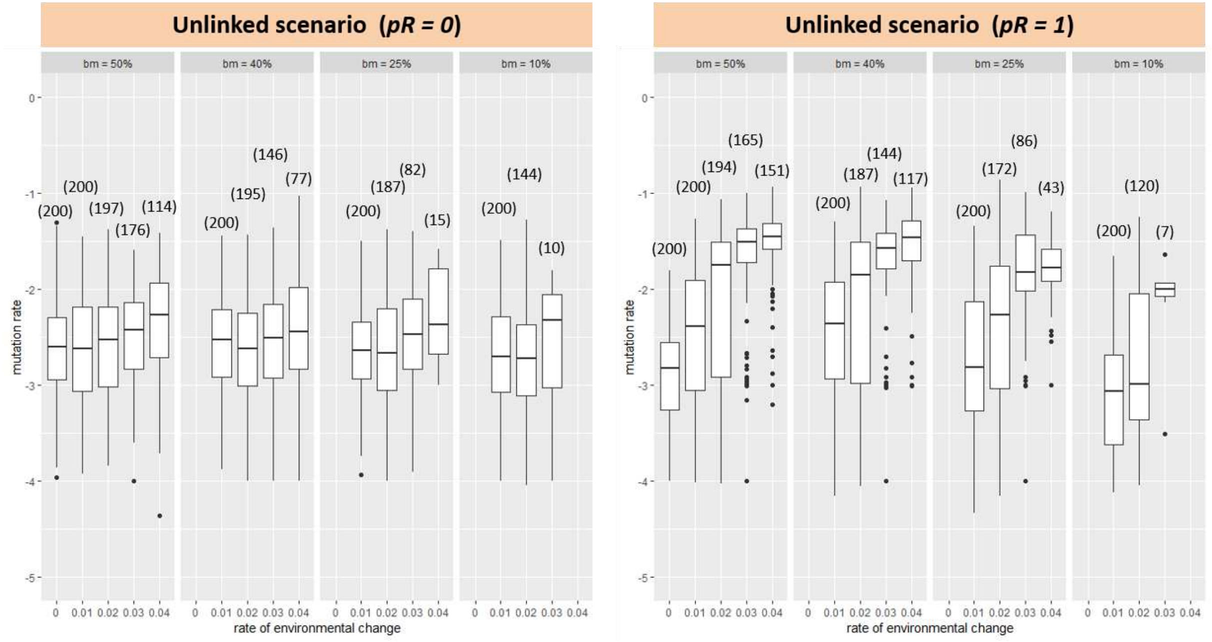


Fig. 3.2 The evolution of the mutation rate under scenarios of directional environmental change, probability of recombination *pR*, and percentage of beneficial mutations *bm*. Each data point corresponds to the mean mutation rate present in the population at the end of each simulation run (200 generations). The scenario of $r = 0$ was performed only for the scenario of $bm = 50\%$. The number of data points per box is shown in parenthesis (selection parameter $\gamma = 2.2$). A weaker selection regime ($\gamma = 3.2$) showed a similar pattern (data not shown).

In general terms, for a population of a sexual species, it seems unlikely for the mutation rate to evolve to higher values under directional climate change scenarios, unless the rate of change is very rapid ($\eta = 0.04$) and the percentage of beneficial mutations is high (50%). This result is robust under different scenarios of environmental stochasticity and noise color (Figure 3A.2, Appendix 3A).

3.5 Discussion

The aim of this study was to investigate whether the mutation rate could evolve to higher values in the course of local adaptation of an isolated population of a sexual species experiencing directional climate change. This work was inspired by a previous study that found adaptive evolution of the mutation rate which advances invasion speed of a sexual population inhabiting an environmental gradient (15). According to our results, the mutation rate can evolve to relatively high values only under conditions of complete linkage or, without such linkage, under the assumption of 50% beneficial mutations. Under complete linkage, the mutation rate can evolve under intermediate to high rates of environmental change, and when the percentage of beneficial mutations is at least 25%. The scenario of complete linkage suggests mutation rates can be expected to evolve in asexual organisms, which is in line with current theory (10,11). For example, it was demonstrated for *Escherichia coli* populations that mutator alleles could be fixed by hitchhiking on beneficial mutations at other loci (12). In a sexual species, scenarios resembling intermediate to complete linkage may occur if the mutator locus is somehow linked to the trait under selection (*e.g.*, by close proximity on the same chromosome), such that it can hitchhike on beneficial mutations occurring on the evolving trait. Scenarios of intermediate linkage ($pR = 0.5$) can also yield slightly elevated mutation rates, relative to the unlinked scenario. However, assuming a definite location of the mutator locus in the genome (as, *e.g.*, a locus encoding for a DNA polymerase), most traits under selection can be expected to be encoded far away from the mutator locus, such that the unlinked scenario seems most appropriate for sexually reproducing species.

On the other hand, under unlinked recombination scenarios, the mutation rate evolved to relatively higher values only under scenarios of 50% beneficial mutations, particularly when the rate of environmental change was fast. When the percentage of beneficial mutations was low (10 and 25%), either there were too few data points (2) to derive any conclusion, or the population went extinct for all runs when the rate of environmental change was increased. Thus, the likelihood of beneficial mutations occurring under scenarios of rapid climate change becomes of high importance for organisms with limited plasticity and standing genetic variation, in order to allow for evolutionary rescue in specialist species. These results are in contrast with those in Cobben et al. (15) where the mutation rate facilitated range expansion and evolved towards higher values even under the assumption of 90% lethal mutations. The distribution of fitness effects in Cobben et al. (15) was symmetric (*i.e.*, *bm = 50%* in our model), and the probability of lethal mutations was independent of this distribution. In our model, given that we implemented the percentage of beneficial mutations *bm* directly into the distribution of fitness effects of mutations, the negative effects of mutations (especially when *bm* was low) became stronger, the higher the rate of directional environmental change. Thus, constraining its evolution to scenarios of high percentage of beneficial mutations. This emphasizes potential outcome differences in studies focused on the evolution of the mutation rate depending on the implementation methods for deleterious mutations. Since our method is consistent with the concept of slightly deleterious mutations (16,17), our simulation of beneficial mutations is presumably more realistic than that in Cobben et al. (15) under scenarios of directional selection. In fact, most IBMs of explicit genetics assume a symmetric distribution for the simulation of beneficial mutations when studying directional environmental change scenarios (4). According to empirical data, however, most mutations are negative, some are neutral, and only few are beneficial (5). The common assumption in IBM eco-evolutionary models of 50% beneficial mutations is therefore highly unrealistic and may overestimate evolutionary rescue (or invasion speed) under directional climate change scenarios. We interpret our results as indication that implementation of beneficial mutation percentages more in line with reality may preclude evolution of elevated mutation rates in sexual species, unless there is strong linkage between mutator and trait locus.

According to our model, the evolution of the mutation rate may be possible in asexual unicellular organisms, provided that inherited differences in the function of repair and replication mechanisms exist which could serve as “mutator”. In sexual unicellular organisms the mutation rate can evolve if the organisms experience high rate of environmental change and the probability of occurring beneficial mutations is high, or if mutator genes happen to occur close to genome sequences coding for the evolving trait, such that they can hitchhike with beneficial mutations at other loci. In multicellular organisms, the mutator locus is expected to be present and affect germ and soma alike. This was not considered in our model and represents a model limitation. In these organisms an increase in genomic mutation rate may lead to tissue damage and reduced survival. In the model, the mutation rate affected only the process of inheritance of the traits into the next generations. Therefore, the mutation rate may still evolve in multicellular organisms as suggested by the model if the effects of increased mutation rates compromise survival after reproduction takes place (15), or unless the mutation rate can be somehow increased for segments of the genome (*e.g.*, traits, locus, germ-line).The later scenario may not be consistent with the mutator locus approach as implemented here (*e.g.*, a locus encoding for a DNA polymerase). However, the immune system of vertebrates is an example of high frequency mutations locally restricted to few genes and cell types in multicellular organisms and that has evolved in response to the constant need of novel mutations in the arm race between host and pathogens (14,24).

Our findings that mutation rates evolve to higher values only with unrealistically high percentages of beneficial mutations or complete linkage seem to be independent from some characteristics of the environmental change, as it was replicated for the different levels of stochasticity or noise color. This is in line with the observation of no systematic variation in the mutation rate among organisms experiencing different habitats (14,25). However, there are environmental conditions (*e.g.*, chemicals, radiation) that produce DNA damage or modify the chemistry of enzymes potentially affecting replication fidelity and promoting mutations (26). Such conditions lead to non-adaptive elevations of the mutation rate. Another potential source of variation in the mutation rate is the difference in condition between individuals in the population. It has been shown that environmental and genetic stress compromise DNA repair mechanisms and therefore, causes individuals to pass on a greater mutation load to their offspring (9,27,28). The phenotypic condition can be directly related to the ability of individuals of overcoming the physiological cost of high-fidelity replication (8). Thus, individuals able to pay the cost of fidelity are expected to reduce the mutation rate down to the drift limit, as further reductions will be effectively neutral (14). Those not able to pay the cost are expected to experience relatively elevated values of the mutation rate (8,14).

In conclusion, considering that 50% beneficial mutations may be an unrealistic assumption, and that recombination is ubiquitous in a sexual species, results in this study suggest that, it is unlikely for the mutation rate to evolve to elevated values in a sexual species experiencing directional climate change scenarios. Instead, mutation rate will be under stabilizing selection at the minimal value allowed by limitations by costs of replication fidelity or limitations imposed by the drift limit, as already proposed in the literature (13). Though the frequency of beneficial mutations remains an elusive quantity (5), empirical estimations of beneficial mutations in *E. coli* seem to be far below the lowest scenario investigated in this model (29). If this observation applies to sexual species as well, the evolution of the mutation rate towards elevated values under sexual recombination will become even less likely. It is important to consider that conclusions derived from this study apply under the assumption of a mutator locus affecting replication fidelity. The presence and action of other mechanisms affecting the mutation rate (*e.g*., epigenetics mechanisms) may affect the results as reported in this study (14,24). Therefore, when the percentage of beneficial mutations is small, and populations are not large enough, sexual species (especially multicellular ones) producing few offspring may be expected to buffer their ability for local adaptation mainly through standing genetic variation and plasticity, provided that movement opportunities are constrained. Future work should focus on understanding the potential role of standing genetic variation, polygenic selection, epigenetics and phenotypic plasticity in the ability for local adaptation of sexual species under scenarios of directional climate change and when the probability of beneficial mutations is low.

3.6. Acknowledgements

We thank Ulrike Schlägel for her support in the development of the method for beneficial mutations based on the distribution of mutations fitness effects. This work was funded by the University of Potsdam.

3.7 References

1. Futuyma DJ, Edwards SV, True JR. Evolution [Internet]. Sinauer Associates; 2005. (Evolution). Available from: https://books.google.de/books?id=rRGNQgAACAAJ

2. Burger R, Lynch M. Evolution and Extinction in a Changing Environment: A Quantitative-Genetic Analysis. Evolution. 1995;49(1):151–63.

3. Bürger R, Krall C. Quantitative-Genetic Models and Changing Environments. In: Ferrière R, Dieckmann U, Couvet D, editors. Evolutionary Conservation Biology [Internet]. Cambridge: Cambridge University Press; 2004. p. 171–187. Available from: doi:10.1017/CBO9780511542022

4. Romero-Mujalli D, Jeltsch F, Tiedemann R. Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions. Reg Environ Change. 2019 Aug 18;(19):1–12.

5. Eyre-Walker A, Keightley PD. The distribution of fitness effects of new mutations. Nat Rev Genet. 2007 Aug;8(8):610–8.

6. Drake JW, Charlesworth B, Charlesworth D, Crow JF. Rates of Spontaneous Mutation. Genetics. 1998;148(4):1667.

7. Baer CF, Miyamoto MM, Denver DR. Mutation rate variation in multicellular eukaryotes: causes and consequences. Nat Rev Genet. 2007 Aug 1;8:619.

8. Sniegowski PD, Gerrish PJ, Johnson T, Shaver A. The evolution of mutation rates: separating causes from consequences. BioEssays. 2000;22(12):1057–66.

9. Sharp NP, Agrawal AF. Evidence for elevated mutation rates in low-quality genotypes. Proc Natl Acad Sci. 2012 Apr 17;109(16):6142.

10. Leigh EG. Natural Selection and Mutability. Am Nat. 1970;104(937):301–5.

11. Johnson T. Beneficial mutations, hitchhiking and the evolution of mutation rates in sexual populations. Genetics. 1999;151(4):1621–31.

12. Shaver AC, Dombrowski PG, Sweeney JY, Treis T, Zappala RM, Sniegowski PD. Fitness evolution and the rise of mutator alleles in experimental Escherichia coli populations. Genetics. 2002;162(2):557–66.

13. Lynch M. The Lower Bound to the Evolution of Mutation Rates. Genome Biol Evol. 2011 Jan 1;3:1107–18.

14. Martincorena I, Luscombe NM. Non-random mutation: The evolution of targeted hypermutation and hypomutation. BioEssays. 2013;35(2):123–30.

15. Cobben MMP, Mitesser O, Kubisch A. Evolving mutation rate advances the invasion speed of a sexual species. BMC Evol Biol. 2017 Jun 26;17(1):150.

16. Ohta T. Slightly Deleterious Mutant Substitutions in Evolution. Nature. 1973 Nov 9;246:96.

17. Eyre-Walker A, Keightley PD, Smith NGC, Gaffney D. Quantifying the Slightly Deleterious Mutation Model of Molecular Evolution. Mol Biol Evol. 2002 Dec 1;19(12):2142–9.

18. Björklund M, Ranta E, Kaitala V, Bach LA, Lundberg P, Stenseth NC. Quantitative Trait Evolution and Environmental Change. PLoS ONE. 2009 Feb 20;4(2):e4521.

19. Kopp M, Matuszewski S. Rapid evolution of quantitative traits: theoretical perspectives. Evol Appl. 2014;7(1):169–91.

20. Vincenzi S. Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. J R Soc Interface [Internet]. 2014 Jun 11;11(97). Available from: http://rsif.royalsocietypublishing.org/content/11/97/20140441.abstract

21. Schwager M, Johst K, Jeltsch F. Does Red Noise Increase or Decrease Extinction Risk? Single Extreme Events versus Series of Unfavorable Conditions. Am Nat. 2006;167(6):879–88.

22. Lynch M, Walsh B. Genetics and Analysis of Quantitative Traits [Internet]. Sinauer; 1998. Available from: https://books.google.de/books?id=UhCCQgAACAAJ

23. Martin G, Lenormand T, Goodnight C. THE FITNESS EFFECT OF MUTATIONS ACROSS ENVIRONMENTS: A SURVEY IN LIGHT OF FITNESS LANDSCAPE MODELS. Evolution. 2006 Dec 1;60(12):2413–27.

24. Odegard VH, Schatz DG. Targeting of somatic hypermutation. Nat Rev Immunol. 2006 Aug 1;6:573.

25. Drake JW. A constant rate of spontaneous mutation in DNA-based microbes. Proc Natl Acad Sci. 1991 Aug 15;88(16):7160.

26. Liu B, Xue Q, Tang Y, Cao J, Guengerich FP, Zhang H. Mechanisms of mutagenesis: DNA replication in the presence of DNA damage. Mutat Res Rev Mutat Res. 2016;768:53–67.

27. Agrawal AF. Genetic loads under fitness-dependent mutation rates. J Evol Biol. 2002 Nov 1;15(6):1004–10.

28. Berger D, Stångberg J, Grieshop K, Martinossi-Allibert I, Arnqvist G. Temperature effects on life-history trade-offs, germline maintenance and mutation rate under simulated climate warming. Proc Biol Sci. 2017 Nov 15;284(1866):20171721.

29. Imhof M, Schlötterer C. Fitness effects of advantageous mutations in evolving Escherichia coli populations. Proc Natl Acad Sci. 2001 Jan 30;98(3):1113.

Appendix 3A

Supporting information to Chapter 3

SUPPLEMENTARY MATERIAL

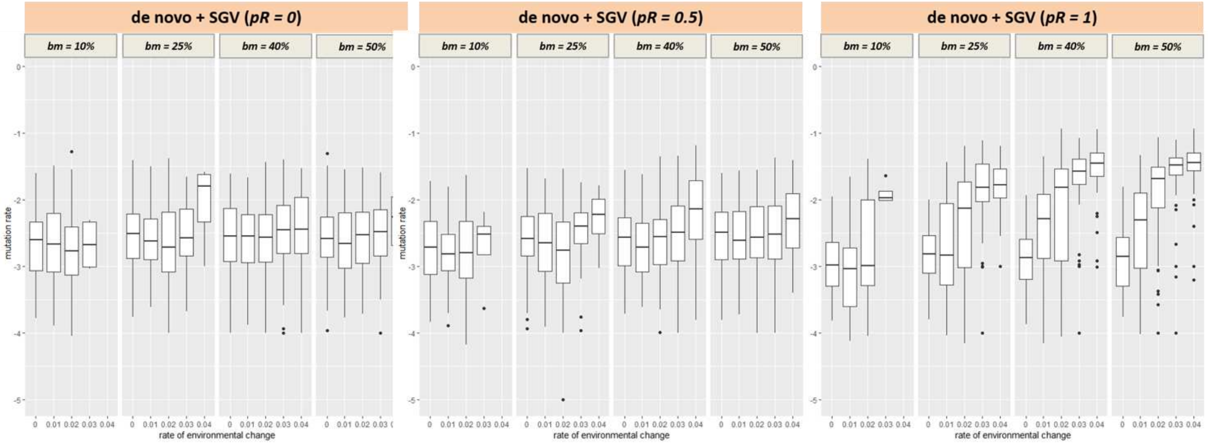


Fig. 3A.1 Evolution of the mutation rate per scenario of beneficial mutations *bm* and scenario of recombination: unlinked (*pR* = *0*), intermediate (*pR* = *0.5*), and complete linkage (*pR* = *1*). Each data point corresponds to the mean mutation rate present in the population at the end of each simulation run (200 generations).

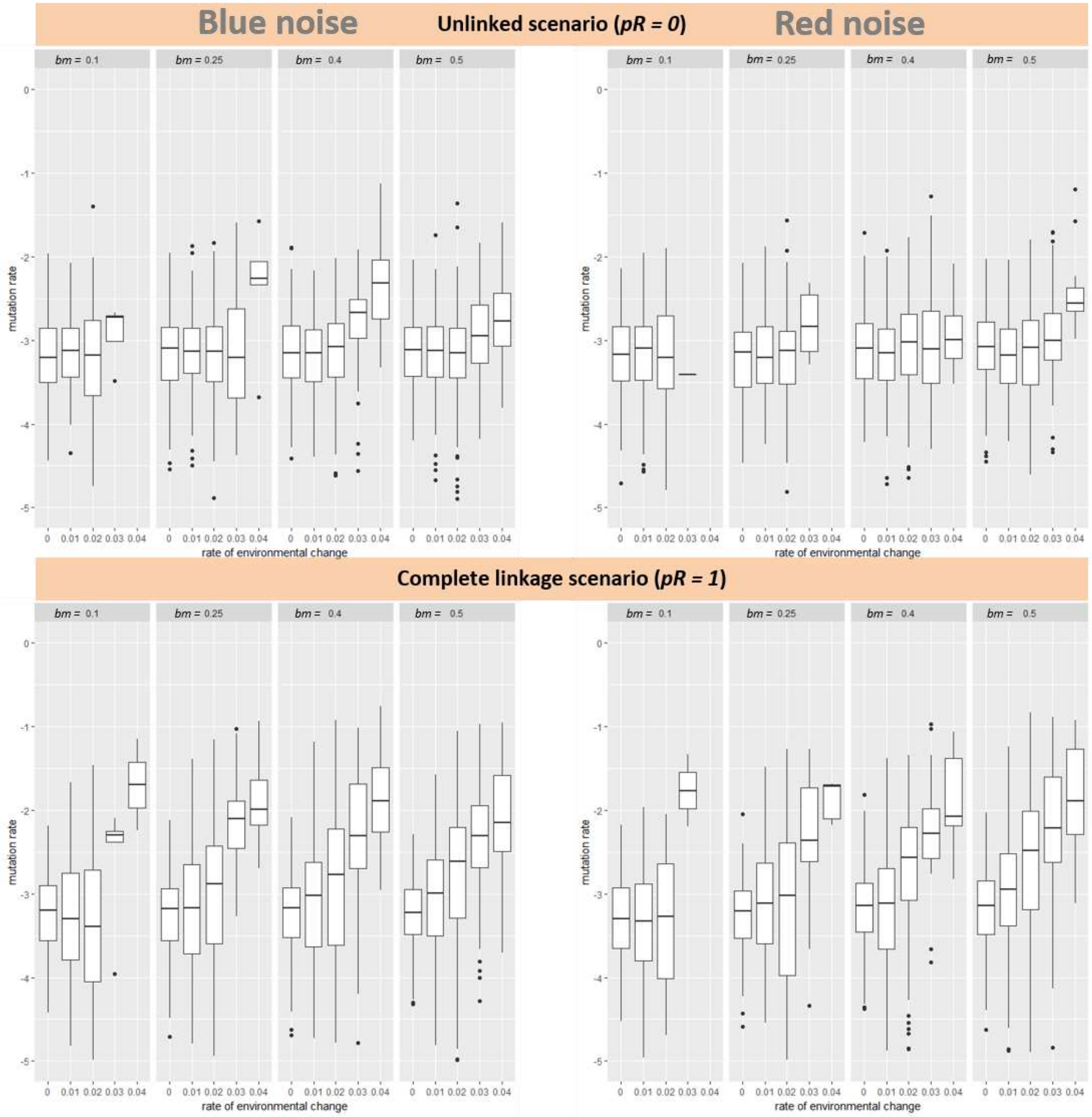
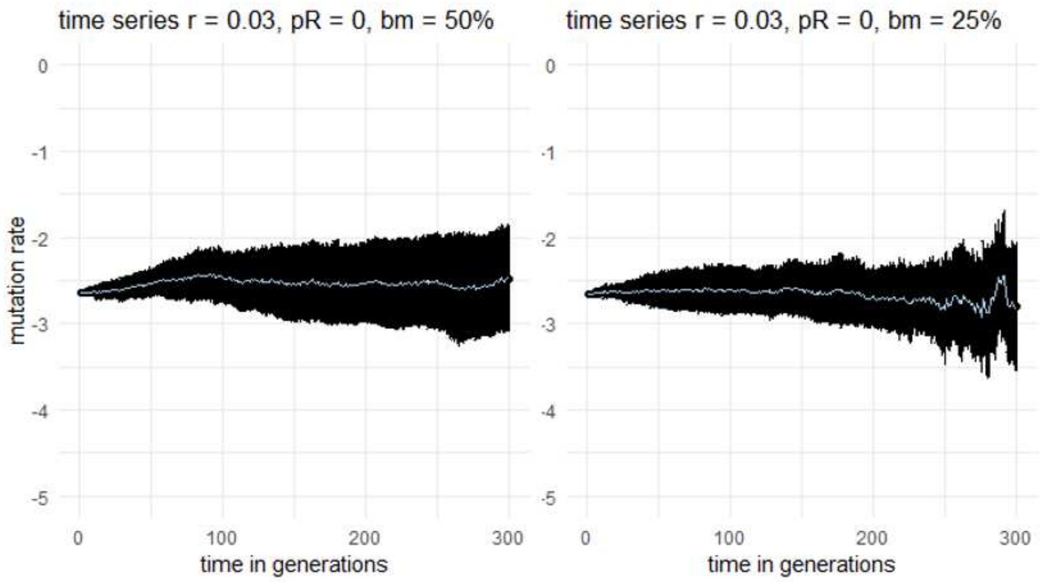


Fig. 3A.2 The evolution of the mutation rate under scenarios of blue (link) and red (right) noise, directional environmental change, probability of recombination *pR*, and percentage of beneficial mutations *bm*. Each data point corresponds to the mean mutation rate present in the population at the end of each simulation run (200 generations).

Unlinked (*pR = 0*)



Complete linkage (*pR = 1*)

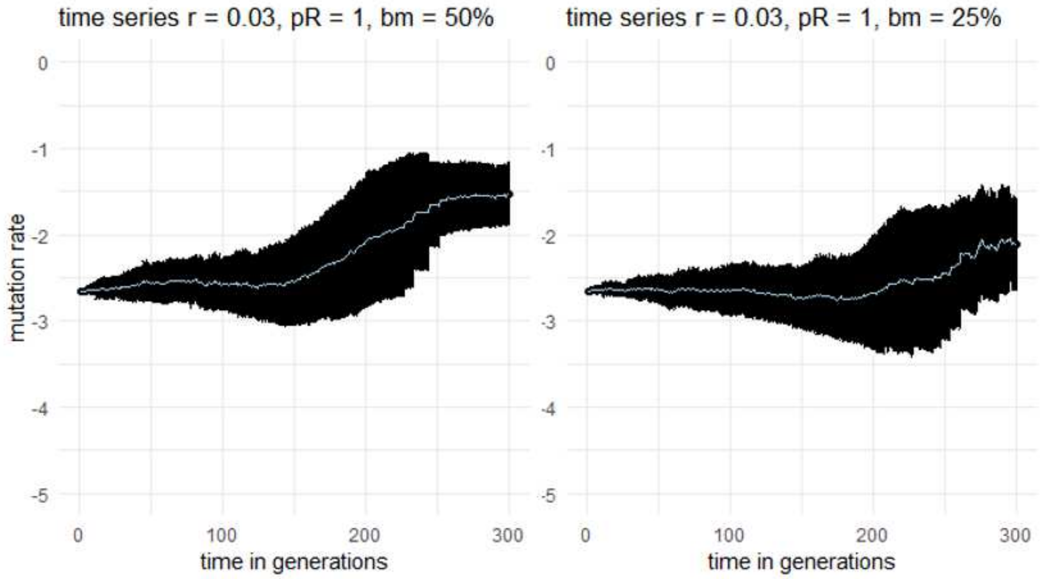


Fig. 3A.3 Trajectory (time series) of the evolutionary dynamics of the mutation rate (mean ± standard deviation from 30 replicates per condition) in a population experiencing rapid directional climate change (r = 0.03), under scenarios of unlinked (upper panel) and complete linkage (lower panel). *pR*: probability of recombination, and *bm*: percentage of beneficial mutations.

Chapter 4

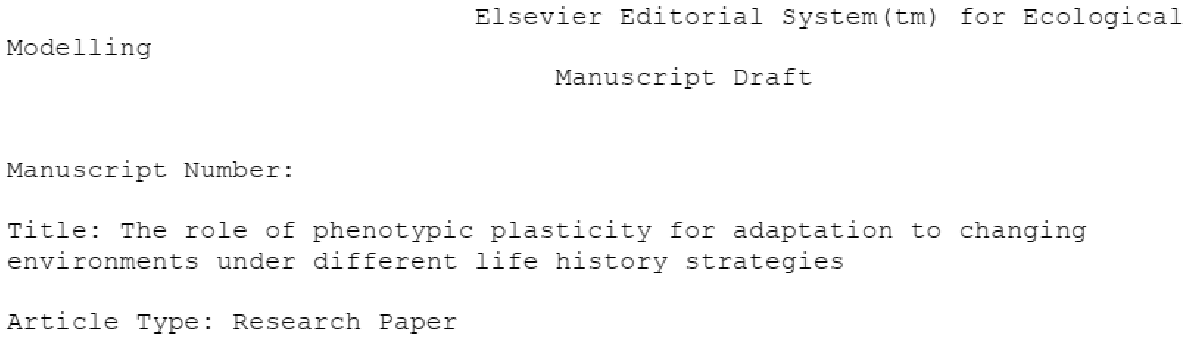
The role of phenotypic plasticity for adaptation to changing environments under different life history strategies

CHAPTER 4

The role of phenotypic plasticity for adaptation to changing environments under different life history strategies

Daniel Romero-Mujalli[1,2], Florian Jeltsch[2,3], and Ralph Tiedemann[1]

This Chapter is submitted to Ecological Modelling



Elsevier Editorial System(tm) for Ecological Modelling

Manuscript Draft

Manuscript Number:

Title: The role of phenotypic plasticity for adaptation to changing environments under different life history strategies

Article Type: Research Paper

[1] University of Potsdam, Evolutionary Biology/Systematic Zoology, Karl-Liebknecht-Strasse 24-25, 14476 Potsdam, Germany

[2] University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlenberg 3, 14476 Potsdam, Germany

[3] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany

4.1 Abstract

Populations can adapt to changing local environmental conditions by genetic changes or phenotypic plasticity. Plastic responses are generally faster and can buffer fitness losses associated to the variable conditions. Most modeling studies investigating this topic has focused on adaptive plasticity. From these, those investigating plasticity under stochastic environmental conditions have focused on the degree of correlation among the cues and the optimum reaction-norm given by the environment (cue reliability). They found that adaptive plasticity is favored when environmental cues are reliable. Yet, how non-adaptive and adaptive plasticity affect population persistence under different forms of stochasticity (different climatic stochasticity or noise color), and scenarios of climate change remain to be studied. Here we present an individual-based eco-evolutionary model and study the relative importance of adaptive and non-adaptive plasticity for populations with different life history strategy, experiencing scenarios of directional climate change and environmental stochasticity. Non-adaptive plasticity was simulated as a random environmental effect on the development of the phenotypic trait, while adaptive plasticity was implemented as linear, logistic, or sinusoidal reaction norms. The last two imposed limits to the plastic response. In the model, life history strategies differed in their reproductive ability and had contrasting population dynamics. The environment was simulated through a climate variable defining a phenotypic optimum moving at a given rate of change (climate change scenarios: no change, slow, medium, rapid). Scenarios of noise color resembling different climatic stochasticity were explored. We found that adaptive phenotypic plasticity promotes population persistence under positively autocorrelated (red noise) environmental stochasticity. In contrast, non-adaptive random phenotypic plasticity was of advantage under high amplitude stochastic changes of environmental conditions (blue noise). Adaptive plasticity was particularly important for life history strategies with low fecundity experiencing scenarios of climate change. Populations producing more offspring could cope with environmental fluctuations relying only on genetic changes or random plasticity, unless the rate of environmental change was too fast.

Keywords

Individual-based models; phenotypic plasticity; reaction-norms; noise color; directional climate change; life strategies

4.2 Introduction

A prevailing challenge in ecology and evolutionary biology is to understand and predict species' responses to environmental change, such as climate change (Chevin et al. 2010; Gonzalez et al. 2013). Populations of species are expected to respond to these changes by local adaptation to novel environmental conditions, shifts in their distributional range while tracking their preferred niche, or local extinction (Franks et al. 2014; Wiens 2016). Particularly, when movement opportunities are constrained, populations are expected to either go extinct or to cope with novel conditions through local adaptation: genetic changes or phenotypic plasticity. Phenotypic plasticity is defined as any non-genetic change of the phenotype induced by changing environmental conditions (Pigliucci 2005; Reusch 2014; Romero-Mujalli et al. 2019). It includes acclimation, developmental plasticity, behavioral flexibility, learning, maternal effects, epigenetics, and random noise (West-Eberhard 2003).

Evolution via genetic changes can rescue a population experiencing a novel environment, provided that enough standing genetic variation exists (Hermisson and Pennings 2005). Among other factors, evolutionary rescue also depends considerably on demographic properties and the generation time of a species (Chevin et al. 2010; Bell 2013). Consequently, a population can go extinct before evolutionary rescue can lead to positive growth rate and recovery (Bell 2013; Ashander et al. 2016). Thus, life strategies where a genetic response is somehow limited, are expected to buffer fitness loss in a novel environment through plastic responses, which are generally faster (Lande 2009; Reusch 2014), and can aid evolutionary rescue through the process of genetic accommodation (West-Eberhard 2003; Schlichting and Wund 2014).

Using individual-based models, a comparison among life history strategies has been performed for the ability of local adaptation through genetic changes (Björklund et al. 2009). However, the role of different types of phenotypic plasticity for persistence under environmental change, relative to different strategies, has not yet been thoroughly investigated. For example, species with relatively high fecundity (large clutch size) may rely less on plasticity as compared to species with clutch-size limited to few offspring, as typical for mammal species. Though it was not the focus of their work, Björklund et al. (2009) observed in their model that r-like life strategists persisted the environmental change the longest (as compared to other life strategies) under scenarios of low heritability in which most variability of the phenotypic trait was developed randomly (random noise).

Phenotypic plasticity has long been considered important for organisms experiencing fluctuating environmental conditions (Scheiner 1993; Via et al. 1995). Models on the evolution of phenotypic plasticity suggest that plasticity evolves in variable environmental conditions, when cues are reliable, and when costs are relatively low (Ghalambor et al. 2007; Chevin et al. 2010; Lande 2014; Hendry 2016; Ashander et al. 2016). Many modeling attempts on phenotypic plasticity under stochastic environmental conditions have focused on the effect of temporal autocorrelation of environmental cues (Reed et al. 2010; Ergon and Ergon 2016; Ashander et al. 2016). Here, environmental cues are often correlated with, but not identical to, the environmental variables affecting fitness (Ergon and Ergon 2016). These models indicate that the evolution of phenotypic plasticity is favored with positively autocorrelated environmental cues (environmental predictability), but not under unpredictable environmental conditions. However, stochastic fluctuations in climatic variables such as temperature lead to another type of environmental stochasticity that have receive less attention regarding the topic of plasticity. Populations experience random fluctuations in environmental conditions (environmental stochasticity), and these fluctuations can differ with regard to their serial autocorrelation between consecutive time units (typically years; Schwager et al. 2006; Björklund et al. 2009). Ecological models have already shown that environmental stochasticity reduces long-term population growth and that the type (i.e., the color) of the stochastic noise differently affect population extinction risk (Heino et al. 2000; Schwager et al. 2006; Björklund et al. 2009; Ferguson et al. 2016). For instance, Mustin et al. (2013) found that extinction risk is expected to be high for populations experiencing directional climate change and inhabiting climates with reddish stochasticity.

Here, we present an individual-based eco-evolutionary model to study the relative importance of adaptive and non-adaptive plasticity for populations with different life histories, experiencing scenarios of various rates of directional climate change and different types of environmental stochasticity (noise color). Thus, this study complements works of phenotypic plasticity under stochastic environmental conditions, since it focusses on a type of stochasticity that has received less attention. In the model we implement non-adaptive and adaptive phenotypic plasticity (with limits). Most theoretical work in the literature have focused on understanding the adaptive nature of phenotypic plasticity (Via and Lande 1985; Nussey et al. 2007; Chevin et al. 2010; Lande 2014), mainly using linear reaction norms (Chevin et al. 2010; Lande 2014; Romero-Mujalli et al. 2019). However, plasticity can be adaptive and non-adaptive (Ghalambor et al. 2007), and reaction norms can be of any shape (Murren et al. 2014). Therefore, our work also adds (secondary objectives) to an improved understanding of the role of non-adaptive phenotypic plasticity and the limits to plasticity. It further contributes to the debate whether adaptive phenotypic plasticity promotes or hinders evolution.

4.3 Methods

To study the effect of adaptive and non-adaptive phenotypic plasticity on population persistence under scenarios of environmental change, we developed an eco-evolutionary individual-based model (IBM) of a geographically isolated panmictic population of a sexual species with non-overlapping generations experiencing stochastic directional climate change. The focus was on local adaptation (no migration was possible). This could resemble a fish population inhabiting a lake, or a plant or animal population inhabiting a highly fragmented environment where movement opportunities are constrained. Populations could differ in fecundity and intrinsic population dynamics (different life strategies). The model also allows for different forms of variation in environmental stochasticity or noise color (e.g., white noise typical for terrestrial locations; red noise, which had been found in coastal and marine habitats, Vasseur and Yodzis 2004).

The model was created using the freely available software platform Netlogo 6.0.2 (Wilensky 1999) and is available for download from https://github.com/danielrm84/PanModel33. A full description of the model that follows the ODD (Overview, Design, concepts, and Details) protocol (Grimm et al. 2006; Grimm et al. 2010) can be found in Appendix 4A. Below, only model features that were used in this research are explained. The sequence of model operations was: update of environmental state, check of degree of local adaptation (as fitness proxy), computation of fecundity, reproduction of adults, inheritance, update of offspring phenotypic values, die-off of adults, and check for extinction before repeating the loop (Fig. 4.1).

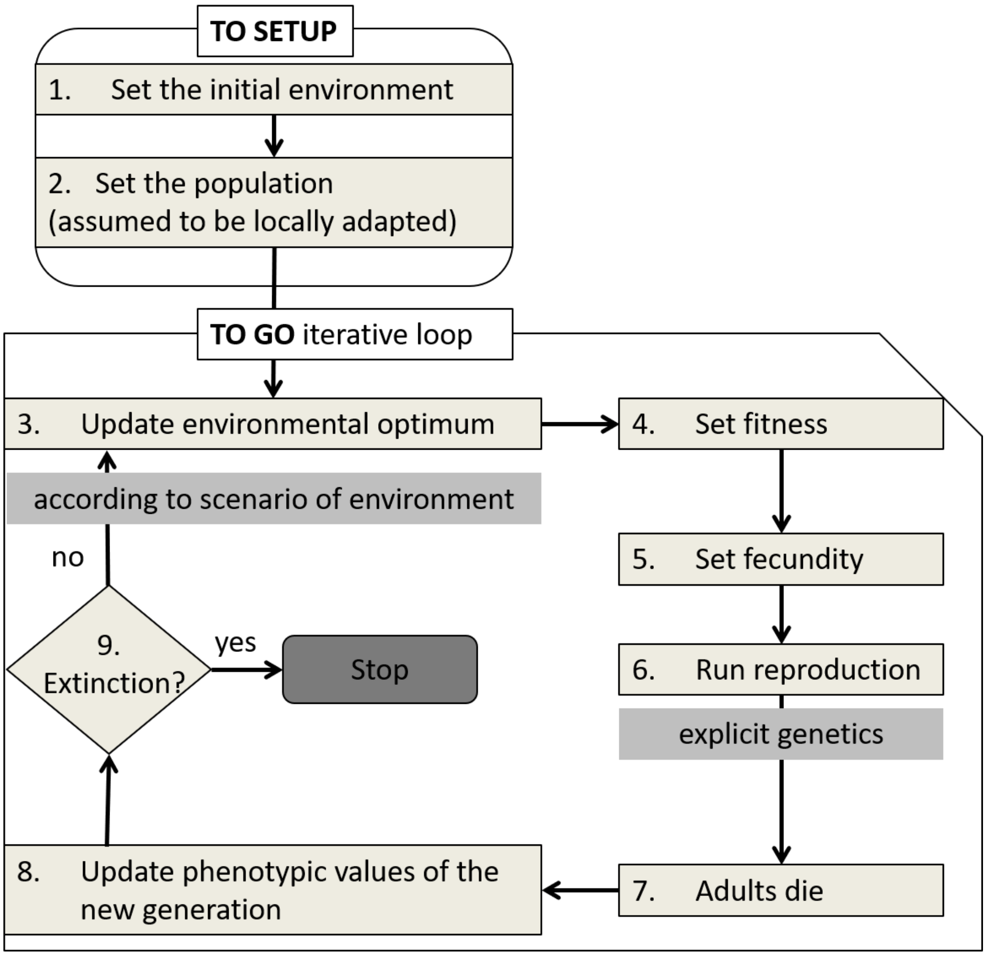


Fig. 4.1 Flowchart diagram of the sequence of model operations.

4.3.1 Landscape

The environment imposed a phenotypic optimum θ_t (hereafter, environmental optimum) which could change at constant speed every generation depending on the simulated scenario of environmental change. Thus, $\theta_t = \theta_0 + \eta\, t$ determined the directional trend of the optimum θ_t in a deterministic environment (no stochasticity). The parameter θ_0 was the initial environmental optimum (when $t = 0$) and η, the rate of environmental change. By varying the parameter η we simulated different scenarios of directional climate change (e.g., no change, slow, medium, rapid climate change). Stochastic colored noise around θ_t was implemented to simulate different scenarios of environmental stochasticity (Fig. 4.2). This method has been recommended as best suiting for the simulation of directional climate change scenarios (Kopp and Matuszewski 2014; Vincenzi 2014).

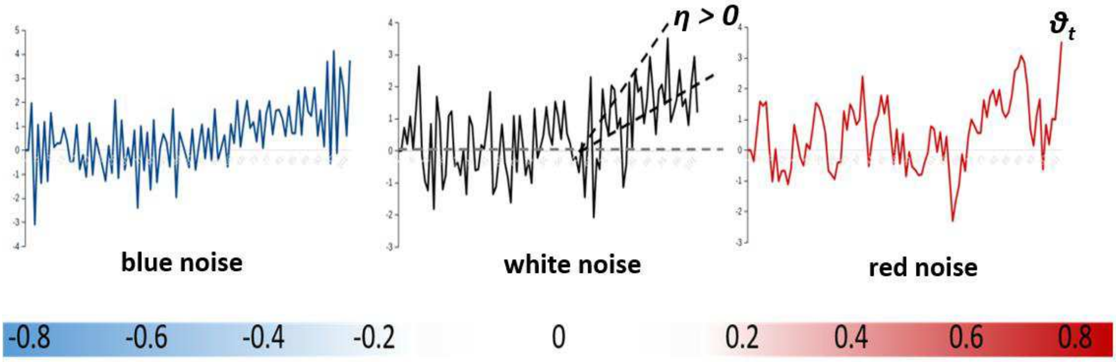


Fig. 4.2 Example of scenarios of directional climate change and environmental stochasticity as simulated in the model. Different forms of stochastic fluctuations (noise color) of the environmental optimum (θ_t) were simulated. They differ in their autocorrelation, i.e., no autocorrelation (white), negative autocorrelation (blue), or positive autocorrelation (red). The parameter η illustrates different rates of directional climate change (no change, slow to rapid change). The color bar shows the range of values explored for the level of autocorrelation (α, see methods).

Stochasticity according to colored noise was implemented such that the environmental optimum was redefined as $\theta_t = \theta^*_t + \phi_t$ where θ^*_t gave the directional trend of the mean environmental optimum as specified above, and $\phi_t = \alpha\phi_{t-1} + \beta\xi_t$, the stochastic noise. The parameter α governed the level of environmental autocorrelation, and therefore, allowed for different forms of stochasticity or noise color as in Björklund et al (2009): $-1 < \alpha < 0$, blue noise; $\alpha = 0$, white noise, and $0 < \alpha < 1$, red noise (Fig. 4.2). Several scenarios of noise color (values of α) where explored, ranging from negatively autocorrelated environmental conditions or blue noise, to uncorrelated (white noise), and positively autocorrelated environmental conditions or red noise (see Table 4.1). The parameter $\beta = \sigma\sqrt{1 - \alpha^2}$ was the adjusted environmental variance for all degrees of autocorrelation, as in (Schwager et al. 2006), and σ^2

$= 1$ was the environmental variance. The parameter ξ_t was a random value, normally distributed with zero mean and unity of variance.

4.3.2 The population

Individuals in the population were characterized by sex, stage (whether adult or juvenile), degree of local adaptation (fitness proxy), fecundity, and an ecological phenotype (evolving trait). The ecological phenotype z had its genetic component a defined by L diploid loci with additive effects, and its environmental component e determining the contribution of phenotypic plasticity in the development of the trait. Thus, $zi = ai + e$, was the ecological phenotype of individual i, where $ai = \sum_{l=1}^{L} nl$, and where nl was the sum of allelic values at locus l. At the beginning of the simulation, the population composed of N individuals was assumed at carrying capacity ($N = K = 1000$) and locally adapted. This means that for each individual organism, alleles coding for its ecological phenotype were drawn from a normal distribution with mean equal to the environmental optimum θ_0 and variance $V = VG / 2L$, where $VG = 0.2$ was the initial genetic variance present in the population, and $L = 1$, the number of loci affecting the phenotypic trait.

4.3.3 Phenotypic plasticity

Four different types or scenarios of phenotypic plasticity were implemented (Fig. 4.3A): random noise, linear reaction norm, sinusoidal reaction norm, and logistic reaction norm. In the model, phenotypic plasticity affected the environmental component e of the ecological phenotype. Random noise has been the most common method in eco-evolutionary IBMs for the representation of an environmental effect on the development of the phenotypic trait (Romero-Mujalli et al. 2019). In this model, we consider random noise as part of non-adaptive phenotypic plasticity. Thus, we could compare the effect of non-adaptive and adaptive phenotypic plasticity on population persistence. In the model, random plasticity assumed *e* to be random and normally distributed with zero mean and variance $VE = \sigma^2$, the environmental variance.

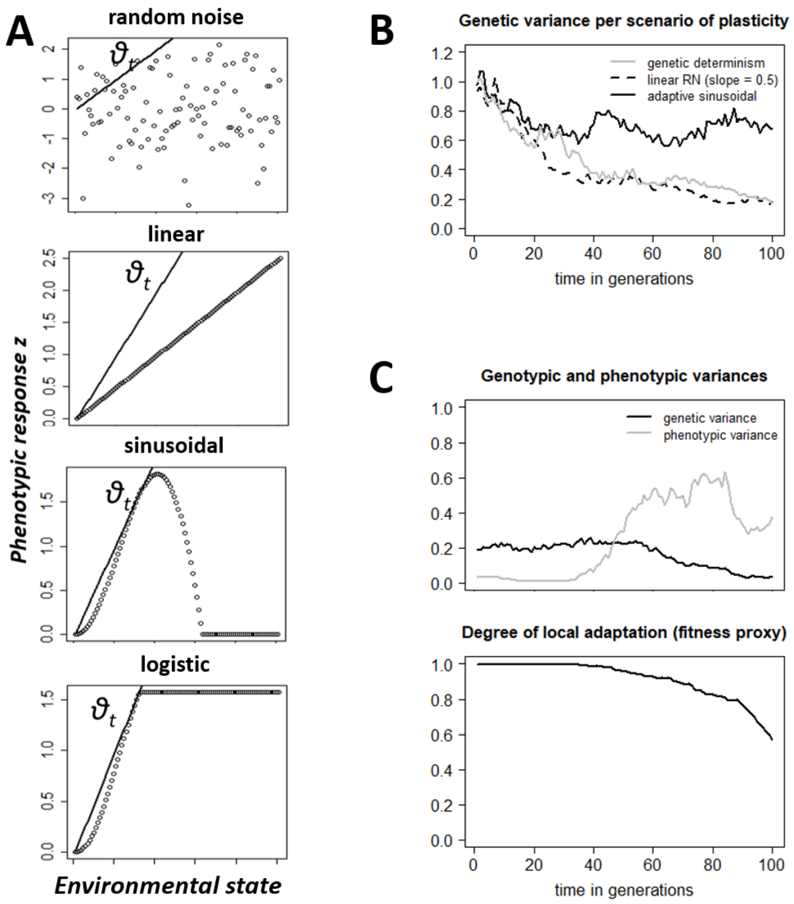


Fig. 4.3 (A) Forms of non-adaptive (random) and adaptive (linear, sinusoidal, logistic) phenotypic plasticity implemented in the model. The black line indicates the moving phenotypic optimum θ_t as given by the environment. Empty circles show the phenotypic response of the organism. (B) Genetic variance present in a population experiencing controlled environmental conditions (no climate change, no stochasticity) per scenario of phenotypic plasticity. In the example, adaptive sinusoidal plasticity maintains the highest genetic variation. The same holds for logistic plasticity (not shown). (C) Time series of the genotypic and phenotypic variances present in a population experiencing deterministic directional environmental change (no stochasticity), under the scenario of adaptive sinusoidal phenotypic plasticity (upper panel). When the population is locally adapted (initial part), there is *developmental canalization* (Posadas and Carthew 2014) of the trait and therefore, less phenotypic than genetic variation. As the environment changes and the population is pushed towards its limits of plasticity, cryptic phenotypic variation arises, and the mean fitness (here, degree of local adaptation) of the population reduces (lower panel).

For the modeling of adaptive phenotypic plasticity, we considered three approaches: the linear reaction norm without a limit, which is the most common approach in the literature (Chevin et al. 2010; Lande 2014; Romero-Mujalli et al. 2019); and two other approaches that account for limits to phenotypic plasticity (Fig. 4.3A). In the literature, most research has focused on costs of plasticity, and very little on its limits (Murren et al. 2015).

In our model, the linear reaction norm defined the environmental component as $e = b\theta_t$; where b is the slope or degree of plasticity, and θ_t the environmental optimum at time t (in generations). Furthermore, the linear reaction norm was assumed to be shallower ($b = 0.5$) and in the direction of the phenotypic optimum θ_t. This emphasized the fact that the linear plastic response was adaptive for the model, and that there was a lag due to the development of the trait (Lande 2009; Chevin et al. 2010; Ashander et al. 2016). It is important to mention that perfect sensing of the environment was assumed for all scenarios of adaptive phenotypic plasticity. The effect of different degrees of sensing was beyond the scope of this work.

The two other methods, logistic and sinusoidal, were designed based on observations from stress tolerance responses for some physiological traits (Jordan and Deaton 1999; Araújo et al. 2014; Solan and Whiteley 2016; Araújo et al. 2016; Wiesenthal et al. 2018), and on behavioral traits. Their plastic response was assumed to be constructive (Laland et al. 2015), relying on feedback with the environment, and in the direction of the environmental optimum (adaptive). This means that they allowed for stable functioning (close to the optimum) despite of the variation at the genetic level. A consequence of this implementation is that they maintain higher genetic variance than the alternative methods even when the population is exposed to a highly controlled environment (e.g., laboratory conditions) for several generations (Fig. 4.3B), which agrees with observations (Maharjan et al. 2006; Fussmann et al. 2007). These methods differed from each other only in the condition that determined the phenotype produced when the limit is exceeded, and were implemented as follows:

$e = \Omega \Delta E$; where Ω was always positive and shaped the plastic response. It was given by $\Omega = sin(|\Delta E|)$. The term ΔE indicated the amount of change with respect to the reference environment $\theta^R = a$, such that $\Delta E = \theta_t - \theta^R$. The parameter a was the genetic component of the phenotype.

For sinusoidal phenotypic plasticity, if the argument of the sine function was greater than π, the environmental component e was set to 0 (the organism fails to develop a plastic response). An example could be snails subject to salinity stress. If the change is too large (compared to the reference environment where plasticity is not needed), snails fail to develop enough physiological response to counter and balance osmotic pressure (e.g., Jordan and Deaton 1999; Wiesenthal et al. 2018). Additionally, in the model sinusoidal plasticity allowed for the appearance of cryptic variation in the population when it was pushed towards the limits (Fig. 4.3C). Cryptic variation refers to genetic variation that normally has little or no effect on phenotypic variation but that under atypical conditions generates phenotypic variation (Paaby and Rockman 2014).

On the other hand, for logistic phenotypic plasticity, if the argument of the sine function was greater than $\pi / 2$; the term ΔE was set to $\Delta E = \pi / 2$ such that a maximum response was reached (saturation). This could resemble plant species expose to different light conditions. After some point of increasing light intensity, a maximum thickness will be reached, and the plant's leaves would not grow any thicker (Wilson and Cooper 1969).

The process of genetic accommodation (West-Eberhard 2003; Schlichting and Wund 2014) was observed for these two methods without the consideration of costs to plasticity.

4.3.4 Degree of local adaptation

After developing the phenotype, adult individuals in the population were subject to stabilizing selection according to the following Gaussian function ((Burger and Lynch 1995):

$$wi = e^{\frac{-(zi - \theta t)^2}{2\gamma^2}}$$

Where wi was the degree of local adaptation (fitness proxy) of individual i, and γ, the width of the function (strength of selection). The closer the ecological phenotype zi was to the optimum θ_t, the better the individual coped with the environmental conditions.

4.3.5 Fecundity and life strategies

The fecundity of individuals in the population was scaled according to their degree of local adaptation after considering density dependence effects, as in Björklund et al (2009):

$$w'i = wie^{\psi(1-\frac{N}{K})}$$

where $w'i$ was the fecundity of individual i, N was the population size and K, the carrying capacity. The parameter ψ described the strength of the density dependence effect. The higher ψ, the stronger was the density dependence effect. Here we implemented three levels of ψ as in Björklund et al. (2009): *0.5*, *1.8* and *2.5*. These three values produced fundamentally different population dynamics (Fig. 4.4A and B).

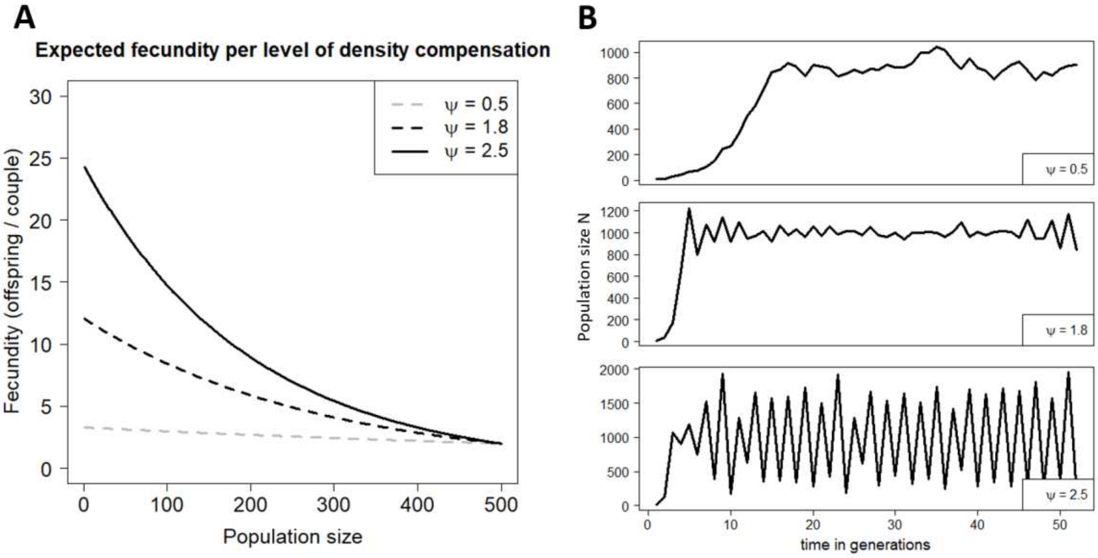


Fig. 4.4 Life strategies as implemented in the model. (A) expected fecundity (λ) per reproductive couple for different values of population size (carrying capacity $K = 500$). When the population size is low, resources are plenty, and well adapted couples can contribute their best in number of offspring (fecundity) for the next generation. (B) Population dynamics per life strategy (values of ψ) in a static environment (no climate change, no stochasticity).

4.3.6 Reproduction

Adult individuals mated randomly with others of opposite sex, with replacement for males only (i.e., lottery polygyny, males could participate in more than one reproductive event). The fecundity of the reproductive couple λ was equal to the sum of the scaled fitness of the partners *i*,*j*:

$$\lambda = w'i + w'j$$

Each couple produced a number of offspring randomly drawn from a Poisson distribution with expectancy λ.

4.3.7 Inheritance

After reproduction, each offspring inherited one strain copy or haplotype from each parent. Only the genetic component (or breeding value) a was inherited. Allele values of the inherited haplotype were picked randomly from the corresponding parental locus (unlinked recombination resp. full linkage equilibrium). Each haplotype could mutate with probability μ of mutation per locus. In case that a mutation occurred, its effect was randomly drawn from a normal distribution with zero mean and variance equals to the effect size of mutations MV, which was an input parameter (Vincenzi 2014). The assumption of a Gaussian distribution is consistent with analysis of mutation effects (Lynch and Walsh 1998; Martin et al. 2006).

All adults died after reproduction (non-overlapping generations). Offspring developed their phenotype according to their genetic and plastic components, and matured into adults, before repeating the loop.

4.3.8 Simulation experiments

With the model we studied the effect of non-adaptive and adaptive phenotypic plasticity on population persistence under scenarios of directional stochastic environmental change. To this end, 200 replicates lasting 100 generations each were performed for different combinations of rate of directional climate change, degree of autocorrelation (noise color), type of phenotypic plasticity (including genetic determinism), and density dependence effect (life strategy) (see Table 4.1). To complement the findings on life strategies of intermediate and strong density dependence effects, additional scenarios of rate of environmental change were performed only for these two strategies. Additional values of the parameter governing the level of density dependence effect were explored only for moderate rate of environmental change with stochasticity. This was done to complement initial results and relate a critical value of fecundity with the relative importance of phenotypic plasticity. The analysis of data and plotting was performed in r v3.4.2.

Table 4.1 Parameter values and description

Parameter	Value	Description
K	1000	Carrying capacity
γ	2.2	Strength of selection
σ^2	1	Variance of the stochastic environment
θ_0	0	Initial environmental optimum
η	0, 0.01, 0.02, 0.03, 0.04 Additional experiment: 0.07	Rate of environmental change
α	-0.8, -0.6, -0.4, -0.2, 0, 0.2, 0.4, 0.6, 0.8	Level of environmental autocorrelation (scenarios of stochasticity)
ψ	0.5, 1.8, 2.5 Additional experiments: 0.6, 0.8, 1.0	Density dependence effect (life strategy)
z	evolving trait	Ecological phenotype
b	0.5	Slope of the linear reaction norm
VG	0.2	Initial genetic variance present in the population
L	1	Number of loci per evolving trait
μ	0.001	Mutation rate*
MV	0.2	Variance of the distribution of mutations fitness effect size
t	100	Time limit per simulation, in generations

* The value of the mutation rate was picked according to results of a simulation model on the evolution of the mutation rate after 300 generations of a population experiencing stochastic environmental conditions (no climate change, and no plasticity, Romero-Mujalli et al. in revision, Chapter 3). In addition this value is within the range of mutation rates used in other simulation models (review in Romero-Mujalli et al. 2019).

4.4 Results

Under scenarios of weak density dependence effect ($\psi = 0.5$), in which breeding pairs in the population could produce relatively few offspring, adaptive phenotypic plasticity played a major role promoting persistence as compared to organisms with higher ψ (Fig. 4.5, 4.6). Particularly for this life strategy, adaptive phenotypic plasticity became of high importance promoting local adaptation under uncorrelated to positively autocorrelated environmental stochasticity (white and red noise). In contrast, under negatively autocorrelated environmental stochasticity (blue noise), adaptive phenotypic plasticity showed poor performance and hindered evolution. Under these conditions, random plasticity (non-adaptive plasticity) and no plasticity at all (genetic determinism) performed the best (Fig. 4.5). However, if the rate of change η was too rapid, adaptive phenotypic plasticity (particularly, linear reaction norm and logistic plasticity) became of advantage for all simulated environmental conditions of noise color (Fig. 4.5).

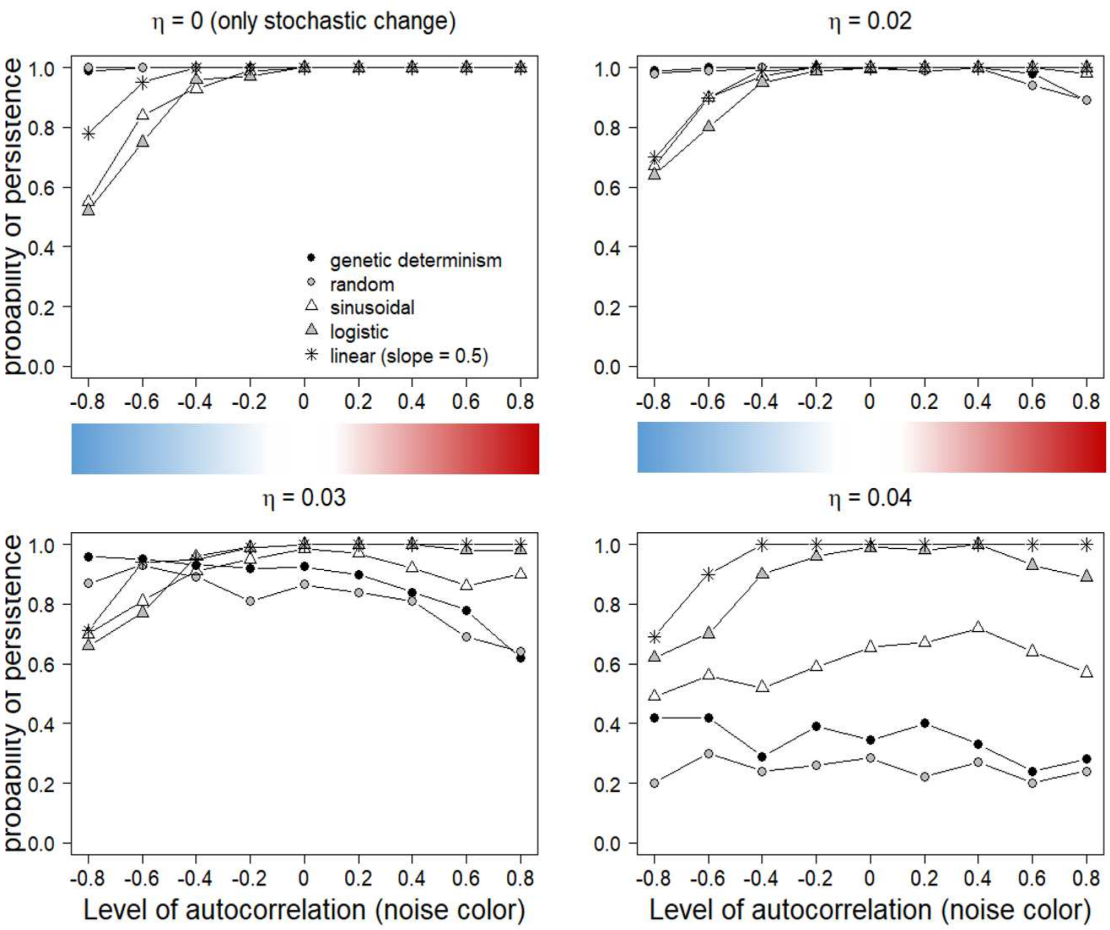


Fig. 4.5 The effect of non-adaptive (random) and adaptive (linear, sinusoidal, and logistic) phenotypic plasticity on probability of persistence (200 replicates, 100 generations each) of a population in which breeding couples are limited to produce relatively few offspring ($\psi = 0.5$, weak density dependence effect). The linear reaction norm had a slope $b = 0.5$. A scenario of genetic determinism (narrow sense heritability $h^2 = 1$) was also simulated. The color bar illustrates the color of the stochastic noise.

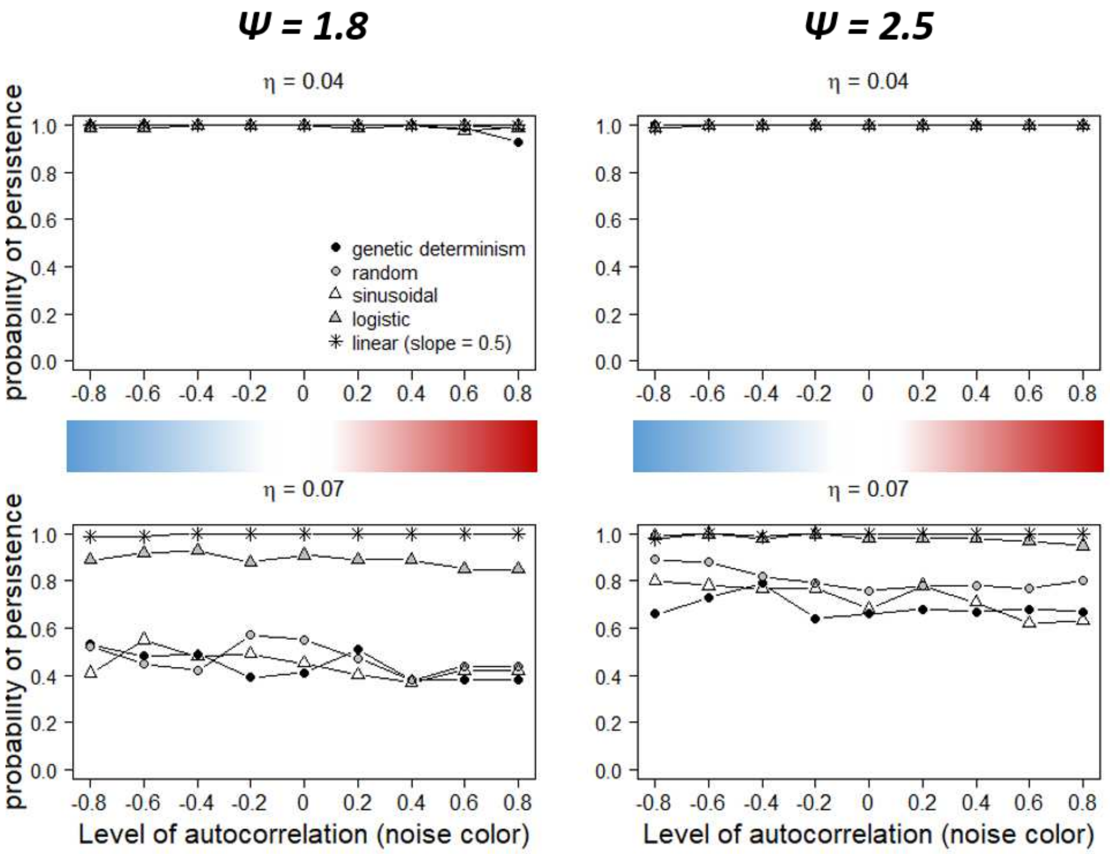


Fig. 4.6 Effect of non-adaptive (random) and adaptive (sinusoidal, logistic, and linear) phenotypic plasticity on the probability of persistence (200 replicates, 100 generations each) of a population of intermediate and strong density dependence effect ($\psi = 1.8$ *and* 2.5, respectively). The linear reaction norm had a slope $b = 0.5$. A scenario of genetic determinism (narrow sense heritability $h^2 = 1$) was also simulated. The color bar illustrates the color of the stochastic noise. Scenarios of $\eta < 0.04$ were not shown, because all treatments led to maximum probability of persistence.

In contrast, results of strong and very strong density compensation ($\alpha = 1.8$ *and* 2.5, respectively) always persisted under conditions of only environmental stochasticity (no directional climate change) and relatively slow to medium rate of environmental change ($\eta = 0, 0.01, 0.02, 0.03$), regardless of the type of environmental stochasticity (noise color). For these life strategies, genetic determinism and all forms of plasticity performed equally well (Fig. 4.7).

Under scenarios of relatively rapid rate of directional climate change, adaptive linear and logistic phenotypic plasticity performed the best for organisms of intermediate and high density dependence effects ($\alpha = 1.8$ and $\alpha = 2.5$) (Fig. 4.6, $\eta = 0.07$). The life strategy with weak density compensation was not included in this analysis, since it always went extinct, except for the scenarios of linear and logistic plasticity. On the other hand, adaptive sinusoidal, non-adaptive random phenotypic plasticity, and genetic determinism showed similar performance across all scenarios of rapid rate of directional climate change, with random plasticity having slightly better performance than the alternatives (Fig. 4.6).

In addition, we tested for the effect of additional progressively increasing parameter values governing the density compensation under similar conditions of moderate environmental change ($\eta = 0.03$). In this scenario, adaptive phenotypic plasticity became relatively important promoting persistence for life strategies populations with $\psi < 0.8$ (Fig. 4.7). This corresponds to life strategies consisting of breeding couples with maximum expected fecundity of $\lambda \leq 4$ offspring.

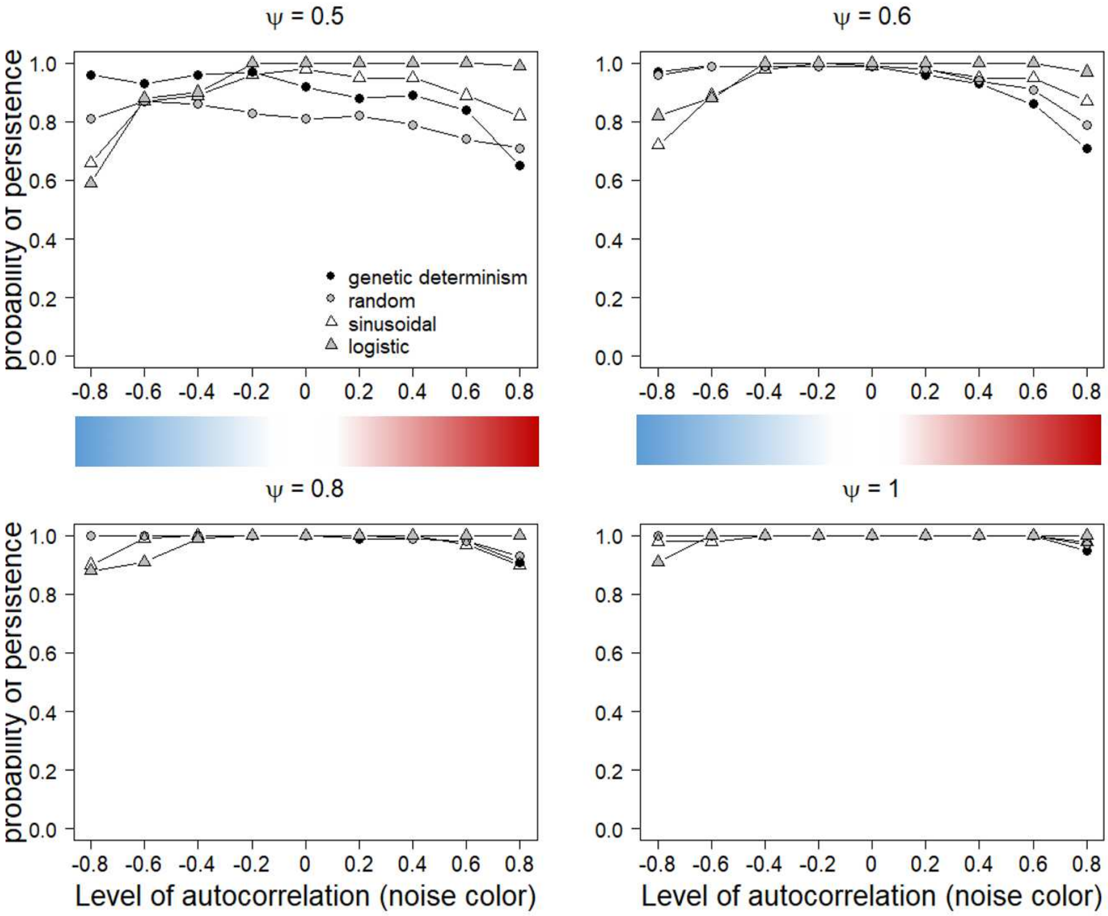


Fig. 4.7 Relative importance of forms of non-adaptive (random) and adaptive (sinusoidal, and logistic) phenotypic plasticity affecting persistence of populations differing in levels of density compensation (ψ) and experiencing moderate rate of directional stochastic environmental change ($\eta = 0.03$). A scenario of genetic determinism (narrow sense heritability $h^2 = 1$) was also simulated. The color bar illustrates the color of the stochastic noise.

4.5 Discussion

The objective of this study was to assess the relative importance of adaptive and non-adaptive plasticity for populations with different life strategy experiencing scenarios of directional climate change and environmental stochasticity (noise color). The simulated environmental conditions, though simplified as in every model, mimic realistic expected scenarios of environmental climate change (Björklund et al. 2009; Kopp and Matuszewski 2014; Vincenzi 2014). Our results show that the relative importance of phenotypic plasticity varies among life strategies. Furthermore, they show that the advantage of non-adaptive and adaptive forms of phenotypic plasticity on population persistence depends on the type of environmental stochasticity (noise color) and the rate of directional climate change.

4.5.1 The role of adaptive phenotypic plasticity

According to our model, adaptive phenotypic plasticity is particularly of advantage when facing positively autocorrelated environmental fluctuations (i.e., red noise), and for a broader spectrum of climatic fluctuations when there is a trend in the mean environmental optimum (directional climate change). Particularly, all forms of adaptive phenotypic plasticity were superior to lack of plasticity for life strategies with relatively slow growth rate (weak density compensation). This life strategy resembles characteristics of many vertebrate species (e.g., birds, and mammals). In contrast, for life strategies with strong density dependence effects and therefore fast growth rate, genetic determinism and all forms of plasticity performed equally well. For these life strategies, only under relatively rapid rates of directional climate change, some forms of adaptive phenotypic plasticity (i.e., linear and logistic phenotypic plasticity) were of advantage. Therefore, if organisms with different life strategies, as simulated in this model, would experience equivalent environmental fluctuations and rates of directional climate change, those where breeding pairs are limited to few offspring are expected to experience stronger selection for the development of mechanisms of adaptive phenotypic plasticity under white and red noise environments. Most fluctuations in climate variables worldwide are characterize by either white or red noise spectra (Vasseur and Yodzis 2004). Linear and logistic phenotypic plasticity are not expected (to evolve in response to selection) for life strategies producing relatively large numbers of offspring, unless they experience relatively rapid rates of directional climate change. A further life history parameter promoting the evolution of adaptive phenotypic plasticity is longevity/generation time, leading to a limited genetic response (Forsman 2014, not tested in our study).

The importance of adaptive phenotypic plasticity for organisms experiencing directional change of the mean environmental optimum, as inferred in our simulations, may equally apply to dispersing and sessile organisms. Dispersing organisms may experience gradual changes in the mean environmental optimum and will benefit from developing adaptive forms of phenotypic plasticity as they expand their range. Especially if density dependence effect is weak, as it occurs for mammal and bird species. Similarly, sessile organisms exposed to seasonal changes in the mean environmental optimum will also benefit from adaptive forms of phenotypic plasticity, particularly if their longevity is long (Borges 2008). Examples are plant species inhabiting temperate regions (Chmielewski and Rötzer 2001), and those experiencing regular yearly cycles of rain, drought and fire at the equator (Fajardo et al. 2005).

4.5.2 The role of non-adaptive phenotypic plasticity

Our model simulated non-adaptive phenotypic plasticity as a random environmental effect on the development of the phenotypic trait (developmental noise, Donaldson-Matasci et al. 2013). Such random phenotypic responses have been reported for several organisms (e.g., plants, Philippi 1993; mammals, McAllan et al. 2012; birds, Visser et al. 2012), particularly regarding timing traits. For example, bats' time of emergence from hibernaculum has important implications on survival and has been thought to occur at random, because predictions on prey availability by individual bats might be based on unreliable environmental cues (Reusch 2019). This random response may be one example of bet-hedging and can be beneficial in the long-term for a population experiencing unpredictable environmental conditions, like drought, floods, and peaks of food availability (Donaldson-Matasci et al. 2013). Our work adds that, even under the assumption of perfect sensing, non-adaptive random phenotypic plasticity can be of advantage over adaptive ones under negatively autocorrelated stochastic environmental conditions (blue noise). According to (García-Carreras and Reuman 2011) temperature climate variables on most continents has become bluer regarding their stochastic/noise pattern. Therefore, random developmental noise may become common for populations experiencing such high amplitude fluctuations (blue noise) in climate variables. Experiments under manipulated environmental uncertainty have already shown that bet hedging strategies can evolve (Beaumont et al. 2009; Graham et al. 2014). However, if the rate of directional climate change is moderate to rapid, our model suggests that all forms of adaptive phenotypic plasticity will become of advantage, even under blue stochastic noise, especially for life strategy populations with relatively slow growth rate (weak density compensation). Apparently then, following adaptively the predictable trend is superior to bet-hedging for high amplitudes of interannual variation. Presumably because of this trade-off, according to our model, such species are expected to face highest risk of extinction under conditions of blue noise and rapid climate change. Organisms with faster growth rate (in our model, intermediate and strong density dependence effects) can rely on non-adaptive plasticity (e.g., bet-hedging) for a broader range of environmental fluctuations.

4.5.3 Phenotypic plasticity and environmental noise

Overall, this work complements previous studies on phenotypic plasticity under stochastic environmental conditions, since it considers stochastic colored noise on the environmental variable affecting fitness. To date, most studies of phenotypic plasticity (and its evolution) under stochastic environmental fluctuations have been focused on the level of autocorrelation among the environmental optimum and the environmental cues sensed by organisms (Reed et al. 2010; Ergon and Ergon 2016; Ashander et al. 2016). Moreover, most of these studies have focused only on adaptive phenotypic plasticity (Nussey et al. 2007). They show that adaptive phenotypic plasticity can only evolve under positive autocorrelation of cues with the environmental optimum (environmental predictability). It is important to note that this type of predictability is not the same as the predictable (red noise) year-to-year pattern of our simulations. Thus, our work adds that adaptive forms of phenotypic plasticity can decrease extinction risk under positively autocorrelated environmental stochasticity (red noise), while extinction risk is expected to be high in the absence of plasticity (Mustin et al. 2013). However, adaptive plasticity can be of disadvantage under negatively autocorrelated environmental stochasticity (blue noise). Under blue noise environmental conditions, adaptive phenotypic plasticity amplifies phenotype-environment mismatches due to the negative autocorrelation in the environmental stochasticity and, therefore, hinders evolution in the long run. In contrast, non-adaptive phenotypic plasticity and genetic determinism increase population persistence under bluish climates. However, adaptive plasticity (particularly, linear and logistic phenotypic plasticity) becomes of advantage for all conditions of stochastic noise when the rate of environmental change is relatively rapid.

4.5.4 On the model implementations of adaptive phenotypic plasticity

In addition, this work accounts for limits to plasticity. Though a thorough analysis of limits to plasticity was beyond the scope of this study, there are some aspects worth consideration. Most studies have focused so far on costs of phenotypic plasticity (Via and Lande 1985; Lande 2009; Chevin et al. 2010; Lande 2014), and very few (if any) on its limits (Murren et al. 2015). Linear reaction norms have no limits, and their evolution can theoretically result in perfect plasticity, which is unrealistic, if no cost is imposed. Therefore, linear adaptive phenotypic plasticity can overestimate probability of persistence. In our simulations this was prevented by having a slope of 0.5 instead of 1. Even so, linear adaptive phenotypic plasticity had the best performance (in terms of increasing population persistence) in comparison to the other methods of adaptive plasticity. Empirically, often costs are weak or difficult to detect, especially for constant characters (van Buskirk and Steiner 2009). Phenotypic plasticity is considered fixed during ontogeny or a constant character when the resulting mature phenotype cannot be further modified by the environment after a period early in life (Romero-Mujalli et al. 2019). In contrast, flexible or labile plasticity occurs when organisms can continuously respond to the environment and, therefore, is presumed to be costlier (Lande 2014). Our work does not distinguish among constant and labile plasticity.

In our model, forms of phenotypic plasticity with limits are assumed to be developmentally constructive (*sensu* Laland et al. 2015) and in the direction of the environmental optimum (adaptive). Constructive development emphasizes the role of regulatory networks enabling highly diverse functional responses through bidirectional interactions of the genotype with the environment (Laland 2015). This assumption leads to stable functioning of the phenotype (close to the optimum) despite of variation at the genetic level (*developmental canalization*, Posadas and Carthew 2014). This feature is associated to redundancy, robustness and adaptability in regulatory networks at the microscopic level (Gerhart and Kirschner 2007; Posadas and Carthew 2014; van Gestel and Weissing 2016). Moreover, it can act as a mechanism that maintain genetic variation, potentially increasing evolvability (van Gestel and Weissing 2016). Furthermore, and in contrast to other forms of plasticity, constructive development of the phenotype can still provide an adaptive response in a novel environment that need not have been pre-screened by earlier selection, as it occurs for learning (Laland et al. 2015; Romero-Mujalli et al. 2017). Additionally, in our model, the mere presence of limits to plasticity (without the consideration of costs) can already lead to genetic accommodation (genes as followers). The process of genetic accommodation occurs when phenotypic variants that are environmentally induced, become genetically determined by natural selection (West-Eberhard 2003; Schlichting and Wund 2014), and has been observed in nature (Schlichting and Wund 2014; Kulkarni et al. 2017). Moreover, our model shows that when the environmental change pushes towards the limits of plasticity, cryptic phenotypic variation may arise. For the model, this means higher phenotypic than genotypic variance, which is a ratio than can be measured in nature. This feature comes along with a reduction in mean fitness of the population (for the model, degree of local adaptation) and could potentially be used as an early warning signal for the unability of a population to sustain environmental change (Boettiger et al. 2013).

4.5.5 Conclusions

Adaptive phenotypic plasticity promotes population persistence under uncorrelated (white noise) and positively autocorrelated (red noise) environmental stochasticity, which applies to the most common climates on earth. This form of plasticity is particularly important for life history strategies in which breeding couples have a limited number of offspring (low fecundity, and hence slow population growth rate). Organisms with life strategies producing more offspring may cope with the environmental fluctuations relying only on genetic changes or random plasticity, unless the rate of environmental change is relatively fast. Models employing linear reaction norms may overestimate persistence because of the absence of limits. In contrast, populations are expected to display non-adaptive random phenotypic plasticity when experiencing high amplitude changes in environmental conditions (blue noise).

In this work, the mechanisms that shape the limits of adaptive plasticity were not explicitly modeled. Therefore, it remains to be studied how molecular mechanisms can shape the limits of plastic responses. It is also important to emphasize that the performance of genetic determinism in the model is affected by the underlying implementation of inheritance. For example, the value of the mutation rate and the assumed distribution of mutations fitness effects can affect the genetic ability of populations to sustain environmental change (Romero-Mujalli et al. 2018, Romero-Mujalli in revision). Future work should investigate the effect of changing these assumptions on the relative importance of phenotypic plasticity for populations experiencing directional stochastic climate change.

4.6 Acknowledgements

We thank Sofia Paraskevopoulou, Sandra Kahl, Remco Folkertsma, and all project members of the Research school "Adaptive evolutionary responses to rapid climate change" at Potsdam University for their valuable contributions, ideas, and feedback for the development of the model. We also thank the students from the course “An introduction to eco-evolutionary modelling using individual-based models” at Potsdam University for their contribution to the model validation and design. We thank Alexis Synodinos for the fruitful discussions on the methods for adaptive phenotypic plasticity. This work was funded by the University of Potsdam.

4.7. References

Araújo CVM, Rodríguez ENV, Salvatierra D, Cedeño-Macias LA, Vera-Vera VC, Moreira-Santos M, Ribeiro R (2016) Attractiveness of food and avoidance from contamination as conflicting stimuli to habitat selection by fish. Chemosphere 163:177–183 . doi: 10.1016/j.chemosphere.2016.08.029

Araújo CVM, Shinn C, Moreira-Santos M, Lopes I, Espíndola ELG, Ribeiro R (2014) Copper-driven avoidance and mortality in temperate and tropical tadpoles. Aquat Toxicol 146:70–75 . doi: 10.1016/j.aquatox.2013.10.030

Ashander J, Chevin L-M, Baskett ML (2016) Predicting evolutionary rescue via evolving plasticity in stochastic environments. Proc R Soc B Biol Sci 283:20161690 . doi: 10.1098/rspb.2016.1690

Beaumont HJE, Gallie J, Kost C, Ferguson GC, Rainey PB (2009) Experimental evolution of bet hedging. Nature 462:90

Bell G (2013) Evolutionary rescue and the limits of adaptation. Philos Trans R Soc B Biol Sci 368: . doi: 10.1098/rstb.2012.0080

Björklund M, Ranta E, Kaitala V, Bach LA, Lundberg P, Stenseth NChr (2009) Quantitative Trait Evolution and Environmental Change. PLoS ONE 4:e4521 . doi: 10.1371/journal.pone.0004521

Boettiger C, Ross N, Hastings A (2013) Early warning signals: the charted and uncharted territories. Theor Ecol 6:255–264 . doi: 10.1007/s12080-013-0192-6

Borges RM (2008) Plasticity comparisons between plants and animals: Concepts and mechanisms. Plant Signal Behav 3:367–375

Burger R, Lynch M (1995) Evolution and Extinction in a Changing Environment: A Quantitative-Genetic Analysis. Evolution 49:151–163 . doi: 10.2307/2410301

Chevin L-M, Lande R, Mace GM (2010) Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. PLoS Biol 8:e1000357 . doi: 10.1371/journal.pbio.1000357

Chmielewski F-M, Rötzer T (2001) Response of tree phenology to climate change across Europe. Agric For Meteorol 108:101–112 . doi: 10.1016/S0168-1923(01)00233-7

Donaldson-Matasci MC, Bergstrom CT, Lachmann M (2013) When Unreliable Cues Are Good Enough. Am Nat 182:313–327 . doi: 10.1086/671161

Ergon T, Ergon R (2016) When three traits make a line: evolution of phenotypic plasticity and genetic assimilation through linear reaction norms in stochastic environments. J Evol Biol 30:486–500 . doi: 10.1111/jeb.13003

Fajardo L, González V, Nassar JM, Lacabana P, Portillo Q. CA, Carrasquel F, Rodríguez JP (2005) Tropical Dry Forests of Venezuela: Characterization and Current Conservation Status. Biotropica 37:531–546

Ferguson JM, Carvalho F, Murillo-García O, Taper ML, Ponciano JM (2016) An updated perspective on the role of environmental autocorrelation in animal populations. Theor Ecol 9:129–148 . doi: 10.1007/s12080-015-0276-6

Forsman A (2014) Rethinking phenotypic plasticity and its consequences for individuals, populations and species. Heredity 115:276

Franks SJ, Weber JJ, Aitken SN (2014) Evolutionary and plastic responses to climate change in terrestrial plant populations. Evol Appl 7:123–139 . doi: 10.1111/eva.12112

Fussmann GF, Loreau M, Abrams PA (2007) Eco-evolutionary dynamics of communities and ecosystems. Funct Ecol 21:465–477 . doi: 10.1111/j.1365-2435.2007.01275.x

García-Carreras B, Reuman DC (2011) An empirical link between the spectral colour of climate and the spectral colour of field populations in the context of climate change. J Anim Ecol 80:1042–1048 . doi: 10.1111/j.1365-2656.2011.01833.x

Gerhart J, Kirschner M (2007) The theory of facilitated variation. Proc Natl Acad Sci 104:8582 . doi: 10.1073/pnas.0701035104

Ghalambor CK, Mckay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407 . doi: 10.1111/j.1365-2435.2007.01283.x

Gonzalez A, Ronce O, Ferriere R, Hochberg ME (2013) Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. Philos Trans R Soc B Biol Sci 368:20120404 . doi: 10.1098/rstb.2012.0404

Graham JK, Smith ML, Simons AM (2014) Experimental evolution of bet hedging under manipulated environmental uncertainty in Neurospora crassa. Proc R Soc B Biol Sci 281: . doi: 10.1098/rspb.2014.0706

Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Pe'er G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rüger N, Strand E, Souissi S, Stillman RA, Vabø R, Visser U, DeAngelis DL (2006) A standard protocol for describing individual-based and agent-based models. Ecol Model 198:115–126 . doi: https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF (2010) The ODD protocol: A review and first update. Ecol Model 221:2760–2768 . doi: 10.1016/j.ecolmodel.2010.08.019

Heino M, Ripa J, Kaitala V (2000) Extinction risk under coloured environmental noise. Ecography 23:177–184 . doi: 10.1111/j.1600-0587.2000.tb00273.x

Hendry AP (2016) Key Questions on the Role of Phenotypic Plasticity in Eco-Evolutionary Dynamics. J Hered 107:25–41 . doi: 10.1093/jhered/esv060

Hermisson J, Pennings PS (2005) Soft Sweeps: Molecular Population Genetics of Adaptation From Standing Genetic Variation. Genetics 169:2335–2352 . doi: 10.1534/genetics.104.036947

Jordan PJ, Deaton LE (1999) Osmotic regulation and salinity tolerance in the freshwater snail Pomacea bridgesi and the freshwater clam Lampsilis teres. Comp Biochem Physiol A Mol Integr Physiol 122:199–205 . doi: 10.1016/S1095-6433(98)10167-8

Kopp M, Matuszewski S (2014) Rapid evolution of quantitative traits: theoretical perspectives. Evol Appl 7:169–191 . doi: 10.1111/eva.12127

Kulkarni SS, Denver RJ, Gomez-Mestre I, Buchholz DR (2017) Genetic accommodation via modified endocrine signalling explains phenotypic divergence among spadefoot toad species. Nat Commun 8:993 . doi: 10.1038/s41467-017-00996-5

Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. Proc R Soc B 282:20151019 . doi: 10.1098/rspb.2015.1019

Lande R (2009) Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. J Evol Biol 22:1435–1446 . doi: 10.1111/j.1420-9101.2009.01754.x

Lande R (2014) Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. J Evol Biol 27:866–875 . doi: 10.1111/jeb.12360

Lynch M, Walsh B (1998) Genetics and Analysis of Quantitative Traits. Sinauer

Maharjan R, Seeto S, Notley-McRobb L, Ferenci T (2006) Clonal Adaptive Radiation in a Constant Environment. Science 313:514 . doi: 10.1126/science.1129865

Martin G, Lenormand T, Goodnight C (2006) THE FITNESS EFFECT OF MUTATIONS ACROSS ENVIRONMENTS: A SURVEY IN LIGHT OF FITNESS LANDSCAPE MODELS. Evolution 60:2413–2427 . doi: 10.1554/06-162.1

McAllan BM, Feay N, Bradley AJ, Geiser F (2012) The influence of reproductive hormones on the torpor patterns of the marsupial Sminthopsis macroura: Bet-hedging in an unpredictable environment. Gen Comp Endocrinol 179:265–276 . doi: 10.1016/j.ygcen.2012.08.024

Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskel MA, Kingsolver JG, Maclean HJ, Masel J, Maughan H, Pfennig DW, Relyea RA, Seiter S, Snell-Rood E, Steiner UK, Schlichting CD (2015) Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. Heredity 115:293–301 . doi: 10.1038/hdy.2015.8

Murren CJ, Maclean HJ, Diamond SE, Steiner UK, Heskel MA, Handelsman CA, Ghalambor CK, Auld JR, Callahan HS, Pfennig DW, Relyea RA, Schlichting CD, Kingsolver J (2014) Evolutionary Change in Continuous Reaction Norms. Am Nat 183:453–467 . doi: 10.1086/675302

Mustin K, Dytham C, Benton TG, Travis JMJ (2013) Red noise increases extinction risk during rapid climate change. Divers Distrib 19:815–824 . doi: 10.1111/ddi.12038

Nussey DH, Wilson AJ, Brommer JE (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evol Biol 20:831–844 . doi: 10.1111/j.1420-9101.2007.01300.x

Paaby AB, Rockman MV (2014) Cryptic genetic variation: evolution's hidden substrate. Nat Rev Genet 15:247

Philippi T (1993) Bet-Hedging Germination of Desert Annuals: Variation Among Populations and Maternal Effects in Lepidium lasiocarpum. Am Nat 142:488–507 . doi: 10.1086/285551

Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? Trends Ecol Evol 20:481–486 . doi: 10.1016/j.tree.2005.06.001

Posadas DM, Carthew RW (2014) MicroRNAs and their roles in developmental canalization. Curr Opin Genet Dev 27:1–6 . doi: https://doi.org/10.1016/j.gde.2014.03.005

Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT (2010) Phenotypic plasticity and population viability: the importance of environmental predictability. Proc R Soc B Biol Sci. doi: 10.1098/rspb.2010.0771

Reusch C (2019) Potential costs, benefits and constraints of responses to recent climate change in bats (PhD Dissertation). University of Greifswald, Germany

Reusch TBH (2014) Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. Evol Appl 7:104–122 . doi: 10.1111/eva.12109

Romero-Mujalli D, Cappelletto J, Herrera EA, Tárano Z (2017) The effect of social learning in a small population facing environmental change: an agent-based simulation. J Ethol 35:61–73 . doi: 10.1007/s10164-016-0490-8

Romero-Mujalli D, Jeltsch F, Tiedemann R (2019) Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions. Reg Environ Change 1–12 . doi: 10.1007/s10113-018-1406-7

Scheiner SM (1993) Genetics and Evolution of Phenotypic Plasticity. Annu Rev Ecol Syst 24:35–68 . doi: 10.1146/annurev.es.24.110193.000343

Schlichting CD, Wund MA (2014) Phenotypic plasticity and epigenetic marking: an assessment of evidence for genetic accommodation. Evolution 68:656–672 . doi: 10.1111/evo.12348

Schwager M, Johst K, Jeltsch F (2006) Does Red Noise Increase or Decrease Extinction Risk? Single Extreme Events versus Series of Unfavorable Conditions. Am Nat 167:879–888 . doi: 10.1086/503609

Solan M, Whiteley N (2016) Stressors in the Marine Environment: Physiological and ecological responses; societal implications. Oxford University Press, Oxford, UK

van Buskirk J, Steiner UK (2009) The fitness costs of developmental canalization and plasticity. J Evol Biol 22:852–860 . doi: 10.1111/j.1420-9101.2009.01685.x

van Gestel J, Weissing FJ (2016) Regulatory mechanisms link phenotypic plasticity to evolvability. Sci Rep 6:24524

Vasseur DA, Yodzis P (2004) The color of environmental noise. Ecology 85:1146–1152 . doi: 10.1890/02-3122

Via S, Gomulkiewicz R, Jong GD, Scheiner SM, Schlichting CD, Tienderen PHV (1995) Adaptive phenotypic plasticity: consensus and controversy. Trends Ecol Evol 10:212–217 . doi: https://doi.org/10.1016/S0169-5347(00)89061-8

Via S, Lande R (1985) Genotype-Environment Interaction and the Evolution of Phenotypic Plasticity. Evolution 39:505–522 . doi: 10.2307/2408649

Vincenzi S (2014) Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. J R Soc Interface 11: . doi: 10.1098/rsif.2014.0441

Visser ME, te Marvelde L, Lof ME (2012) Adaptive phenological mismatches of birds and their food in a warming world. J Ornithol 153:75–84 . doi: 10.1007/s10336-011-0770-6

West-Eberhard MJ (2003) Developmental Plasticity and Evolution. Oxford University Press, New York

Wiens JJ (2016) Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. PLOS Biol 14:e2001104 . doi: 10.1371/journal.pbio.2001104

Wiesenthal AA, Müller C, Hildebrandt J-P (2018) Potential modes of range shifts in euryhaline snails from the Baltic Sea and fresh water lakes in northern Germany. Hydrobiologia 811:339–350 . doi: 10.1007/s10750-017-3501-z

Wilensky U (1999) NETLOGO. Centre for Connected Learning and Computer-Based Modelling, Northwestern University, Evanston, IL

Wilson D, Cooper JP (1969) Effect of Light Intensity During Growth on Leaf Anatomy and Subsequent Light-Saturated Photosynthesis Among Contrasting Lolium Genotypes. New Phytol 68:1125–1135

Appendix 4A

Supporting information to Chapter 4

ODD protocol: eco-evolutionary model of local adaptation

i) Purpose

The purpose of the model is to understand the potential for local adaptation of different kinds of populations of organisms or life strategies under scenarios of environmental change. The model was programmed in Netlogo and designed for hypothesis testing, theory development and for communication and learning. A manual explaining how to install and use the model can be found on https://github.com/danielrm84/PanModel33.

ii) Entities, state variables and scales

What kinds of entities are in the model?

There are two kinds of entities: individuals or turtles (in Netlogo, individuals are called turtles), and patches describing the environment.

By what state variables, or behavioral attributes, are these entities characterized?

Turtles are characterized by sex, stage (whether adult or juvenile), fitness, fecundity, and their phenotype with its genetic and environmental components.

Patches contain two state variables: the mean environmental optimum, which is the optimum phenotype as given by the environment, and its environmental variance. Patches also contain variables recording the degree of maladaptation of the population, and whether extinction occurred, and if “true”, at what time (in generations).

The model has two modules: the Ecology and the Evolution modules. The former governs how the phenotype of organisms interacts with the environment; the latter, how the phenotype is produced. In the Ecology module, the study organism is further characterized by two global parameters: one governing whether it is a specialist, moderate or generalist organism (in our simulations we only considered moderate organisms); and the other, affecting the strength of the density dependence effect, which impacts on the resulting population dynamics (e.g., *r* or *K* strategists). In the Evolution module, global parameters define the number of loci, heritability (only works for standard model with no phenotypic plasticity), initial genetic variance, mutation probability, mutation effect-size and percentage of beneficial mutations. The Evolution module also includes phenotypic plasticity which can be set to: no-plasticity (genetic determinism: phenotype determined by genetic component only), random, linear reaction-norm, or adaptive (with two shapes, logistic and sinusoidal).

What are the temporal and spatial resolutions and extents of the model?

The model is spatial explicit (2D), though patches are currently equivalent in terms of the environmental state. In our work we focused on local adaptation, thus, space to our model was spatially implicit. However, the model is implemented such that it can facilitate future simulations of spatial heterogeneity (e.g., patches differing in quality). The time is discrete, and each time step is a generation. By default, simulations last for 100 generations. The user can modify this parameter value in the user interface.

***iii*) Process overview and scheduling**

What entity does what and in what order?

The iterative loop each generation runs according to the following pseudo-code:

```
1. ask patches [ update-optimum ]
2. ask turtles
   [
         set fitness
         set fecundity
   ]
3. ask turtles [ reproduce ]
4. Observer: < adults die >
5. ask turtles [ update-phenotype ]
6. Observer: < check extinction >
7. Observer: < repeat the loop >
```

This scheme is also shown in Fig 1 of the manuscript (flowchart).

***iv*) Design concepts**

- Emergence

What emerge from the model (rather than being imposed)?

The adaptive response of the population emerges from the model. Population-level attributes as the heritability of the evolving trait and the additive genetic variance can also emerge, rather than being imposed, depending on the chosen experimental setup. An important model output is whether the population goes extinct or can sustain the simulated scenario of environmental change. After considering several replications, this result can lead to the calculation of the probability of persistence.

- Adaptation

How do agents adapt to improve their fitness (directly and indirectly)?

Turtles can adapt to the environment by means of genetic changes (evolution). Plasticity, conceived as a non-genetic environmentally induced phenotypic response, can also affect the ability of organisms for local adaptation. Changes in parameters values governing the genetic properties and the plasticity of organisms, can affect their ability to locally adapt to the simulated environmental conditions.

- Fitness

What are the goals of the agent (or turtle)? What determines its survival?

The closer a turtle is to the environmental optimum, the higher its degree of local adaptation (fitness proxy). Agents that perform well in their environment can contribute with more offspring for the next generation (higher fecundity). The fecundity is affected by density dependence effects. Currently only limits to phenotypic plasticity are considered. Costs of plasticity are not yet implemented. One alternative could be to implement costs to plasticity in terms of fecundity costs.

- Prediction

How do agents predict the consequences of their decisions? Use of learning, memory, environmental cues, embedded assumptions

The concept of prediction is not explicitly considered. There is no learning in the model. Though it can be implemented into the functions of phenotypic plasticity.

- Sensing

What are agents assumed to know or perceive when making decisions?

Is the sensing process itself explicitly modeled?

The sensing process itself is not explicitly modeled. When phenotypic plasticity is assumed to be linear reaction norm, or adaptive, the ability of sensing the environment is assumed to be equal and reliable for all turtles.

- Interaction

What forms of interactions among agents are there?

Turtles interact indirectly via competition for resources and directly through mating. Density dependence effects affect the fecundity of the turtles. The parameter governing the carrying capacity of the environment can be modified in the user interface to allow for populations differing in the maximum size they can reach.

Turtles mate randomly with others of opposite sex, and each couple pass on its genetic contribution to its offspring. Variations in the genetic material occur by recombination and mutations.

- Stochasticity

Justification for any stochasticity in the model.

Stochasticity plays a role in setting the environmental state, in reproduction and in the process of inheritance, and when plasticity is random. The environmental optimum changes every time step according to a given rate of change η. The user can select among different kinds of noise color governing the stochasticity of the environment (blue, white, and red noise). The user can also select to use a deterministic environment. During reproduction the number of offspring is randomly drawn from a Poisson distribution. The process of inheritance is stochastic through the processes of mutation and recombination.

How are stochastic processes (based on pseudorandom numbers) used in the model and why?

Environmental stochasticity. The environmental state θ_t can be stochastic according to the chosen noise color and level of autocorrelation α (Schwager et al. 2006):

$\theta_t = \theta_0 + \eta\, t$ directional change

Where θ_0 is the initial environmental optimum (when $t = 0$) and η is the rate of environmental change. Stochasticity according to colored noise is implemented as follows:

$\theta^*_t = \theta_t + \phi_t$ directional change with noise ϕt and stochastic environmental optimum θ^*_t.

$\phi_t = \alpha\phi_{t-1} + \beta\xi_t$

The autocorrelation coefficient α indicates the level of environmental autocorrelation and therefore the noise color: $-1 < \alpha < 0$, blue noise; $\alpha = 0$, white noise, and $0 < \alpha < 1$, red noise.

The parameter β determines the environmental variance,

$\beta = \sigma\sqrt{1-\alpha^2}$, as in Schwager et al. (2006), where σ^2 is the environmental variance (input parameter).

The parameter ξ_t is a random value, normally distributed with zero mean and unity of variance.

Environmental stochasticity applies for both, directional trend of the mean environment (climate change) and cyclic environmental change.

Mating. Sex is randomly set according to a Bernoulli distribution with probability $p = 0.5$. Individuals mate randomly (males can participate in more than one reproductive event).

Inheritance. In the model, the genetics is implemented according to two common methods: implicit and explicit. In our work, we used the explicit genetics method. Stochasticity operates slightly different for these two methods:

Implicit genetics. The genetic component of the offspring is randomly drawn from a normal distribution centered on the mean parental value, and with variance equal to half the additive genetic variance, plus the variance potentially introduced by mutation or mutational variance (Ayllón et al. 2016; Vincenzi, De Leo, and Bellingeri 2012).

Explicit genetics. The genetic component results from the additive allele effects of the explicitly simulated loci. Alleles values can change due to mutations and recombination. In the model individuals are diploid, each locus receiving one allele from each parent. Parental alleles are picked randomly from each locus in the chromosome (freely recombining or unlinked bi-allelic loci) (Bridle et al. 2010; Vincenzi 2014). Mutations occur randomly according to a Bernoulli distribution with probability μ. In case that a mutation occurs, its effect is randomly drawn from a normal distribution with zero mean and variance equals to the effect size of mutations, which is an input parameter (Vincenzi 2014). The mean of the distribution of effect size can change depending of the percentage of beneficial mutations. The assumption of a Gaussian distribution is consistent with analysis of mutation effects (Lynch and Walsh 1998; Martin, Lenormand, and Goodnight 2006).

Environmental effect on the phenotype. For the standard model, the environmental effect in the development of the trait is assumed to be random and normally distributed with zero mean and a variance VE that can be either fixed (input parameter) or computed as a function of the heritability and the additive genetic variance. Given the value for the narrow-sense heritability

$h^2 = \frac{VA}{VP}$; where VA and VP are the additive genetic variance and the phenotypic variance respectively,

$$VE = \frac{VA}{h2} - VA$$

If the user decides to account for any form of phenotypic plasticity as simulated in the model, heritability is no longer constant, but an emerging property.

Are stochastic processes used,

to initialize the model?

In the initial population, the genotype of each organism is created randomly and assumed locally adapted. Implicit genetics: for each organism, the value for its genetic component is drawn from a normal distribution with mean equal to the environmental optimum and variance equal to the initial additive genetic variance. Explicit genetics: for each individual organism, alleles coding for its phenotype were drawn from a normal distribution with mean equal to the environmental optimum θ_0 and variance V = VG / 2L, where VG was the initial genetic variance present in the population, and L the number of loci affecting the phenotypic trait. Then, the genetic component along with the selected method for phenotypic plasticity build up the phenotype of the organism.

- Collectives

Grouping of individuals.

Collectives are not represented in the model.

- Observation

What outputs are needed to test the model and to solve the problem the model was designed for?

The model was designed to investigate on the ability of different types of organisms for local adaptation to novel local environmental conditions. This can be assessed by monitoring trends overtime in population size, degree of local adaptation, genetic and phenotypic variances, match of the population mean phenotype with the environmental optimum, and by recording extinction events. After several replications, the probability of persistence can be computed for each kind of organism and each scenario of environmental change.

What outputs from the model are needed to observe its internal dynamics as well as its system-level behavior?

The user interface already includes plots showing the internal real time dynamics of the simulation. This includes the genotypic and phenotypic distributions in the population in relation to the environmental optimum. The system-level behavior can be monitored through time series plots describing the population abundance, genetic and phenotypic variances; and by a panel monitoring the degree of local adaptation of the population.

What tools (graphics, file output, data on individuals, etc.) are needed to obtain these outputs?

The user interface already includes the above mentioned plots for real time monitoring of simulation runs. Netlogo software allows exporting plot data in *.csv format for further analysis. In addition, simulation experiments that involve several replicates and systematic variations of model settings can be run using the *BehaviorSpace* tool of Netlogo. The resulting output file (*.csv) can be opened with the preferred program (e.g., R) to compute, for example, the probability of persistence over the selected time span (in generations).

v) Initialization

What is the initial state of the model world? How many entities? What are the exact values of their state variables (or were they set stochastically)?

The initialization of the model world or setup, includes the following:

- The initial environmental state is set to its default initial value. This means that the patch optimum is set to zero (initial environmental optimum).

- *N* agents are created (by default *N = 1000*) and the population is assumed to be locally adapted. Therefore, the resulting mean phenotype of the population is centered on the initial environmental optimum.
- The genetic component of the phenotype is set according to the selected method of genetics (explicit or implicit).
- Phenotypic plasticity is set according to the preferred method (standard model, random, linear reaction norm, adaptive logistic or adaptive sinusoidal).
- The phenotype of the turtles (individuals) is then computed as a linear additive effect of its genetic and environmental or plastic components.

Since the initialization involves stochasticity, initial conditions can vary among simulations, especially when the population size is small.

Are the initial values chosen arbitrary or based on data? (reference to those data should be provided)

The initial values can be chosen arbitrary or can be based on data. For example, the mutation probability, mutation effect-size, number of loci, and heritability of the trait are parameter values that can be set according to data.

***vi*) Input data**

Does the model use input from external sources such as data files or other models to represent processes that change over time?

There are two versions of the model. The one that considers the percentage of beneficial mutations (full version) uses r resources when setting the initial conditions. The other version does not use r resources and therefore cannot simulate scenarios of percentage of beneficial mutations. However, this version is easier to install and use.

***vii*) Submodels**

What, in detail, are the submodels that represent the processes listed in “Process overview and scheduling”?

What are the model parameters, their dimensions, and reference values?

How were submodels designed or chosen, and how were they parameterized and then tested?

- Set the initial environment

The initial environmental optimum is set to zero.

- Set the initial population

In the initial population, the phenotype of each organism is created randomly and assumed locally adapted. Explicit genetics: this means that for each organism, the value for its genetic component is drawn from a normal distribution with mean equal to the environmental optimum θ_0 and variance equal to the initial additive genetic variance. Explicit genetics: for each individual organism, alleles coding for its phenotype were drawn from a normal distribution with mean equal to the environmental optimum θ_0 and variance V = VG / 2L, where VG was the initial genetic variance present in the population, and L, the number of loci affecting the phenotypic trait. The phenotype *z* is then computed as,

$$z = a + e$$

where *a* and *e* are the genetic component and the environmental effect or phenotypic plasticity in the development of the trait, respectively. The value of the environmental effect *e* depends on the selected method for phenotypic plasticity. The standard model and random plasticity assume *e* to be random and normally distributed with zero mean and variance *VE* that can be either fixed (input parameter in the case of random plasticity) or computed as a function of the heritability and the additive genetic variance (standard model). Given the value for the narrow-sense heritability $h^2 = \frac{VA}{VP}$; where VA and VP are the additive genetic variance and the phenotypic variance respectively,

$$VE = \frac{VA}{h2} - VA$$

For the method linear reaction norm, $e = b\theta_t$; where b is the slope or degree of plasticity and θ_t the environmental optimum at time t (in generations).

The two methods of adaptive phenotypic plasticity differ only in the condition that determine when the function is truncated – and therefore differed in what occurs beyond the limits – and were implemented as follows:

$e = \Omega\Delta E$; where Ω is always positive and shapes the plastic response, as it is given by $\Omega = sin(|\Delta E|)$. The term ΔE indicates the amount of change with respect to the reference environment $\theta^R = a$, such that $\Delta E = \theta_t - \theta^R$. The parameter a is the genetic component of the phenotype.

For sinusoidal phenotypic plasticity, if the argument of the sine function is greater than π, $e = 0$ (the organism fails to develop a plastic response). On the other hand, for logistic phenotypic plasticity, if the argument of the sine function is greater than $\pi / 2$; the term ΔE is set to $\Delta E = \pi / 2$ such that a maximum response is reached (saturation).

These two methods were designed based on observations from stress tolerance responses for some physiological and behavioral traits (Araújo et al. 2014; Jordan and Deaton 1999; Solan and Whiteley 2016).

- Update environmental optimum

The model allows for simulating directional environmental change, which imposes a trend on the mean environmental variable (climate change), and cyclic or seasonal environmental change. Seasonality was not investigated in our work, and represents a topic for future research. Stochasticity applies for both scenarios of environment. For climate change, the environmental optimum θ_t changes at rate η per iteration. In the model, one iteration is equivalent to one generation. This corresponds to what is expected for a climatic variable as temperature in the presence of climate change (Kopp and Matuszewski 2014). The model also allows for simulating the environment as mentioned above under scenarios of increasing variance at rate ρ per generation. This leads to the increased frequency of extreme events, as droughts, floods, and heat waves that can also be associated to climate change (Vincenzi 2014; Vincenzi, De Leo, and Bellingeri 2012). Thus, there are two main scenarios of environmental change: climate change and cyclic environment, both with option to account for extreme events. Environmental stochasticity is further simulated adding colored noise around the mean value of the environmental optimum. Thus, the implemented scenarios of environment are:

Climate change scenario:

$\theta_t = \theta_0 + \eta_t$ where θ_0 is the initial environmental optimum (when $t = 0$) and η is the rate of environmental change.

Cyclic environmental scenario:

$\theta_t = A\sin(2\pi t / T)$; where A governs the amplitude and T the period of the wave, and t, the time (in generations) (as in Bürger and Krall 2004).

The stochasticity was implemented as explained above within *Environmental stochasticity*.

- Set fitness

The model assumes Gaussian stabilizing selection acting on a single quantitative character z with the optimum phenotype θ_t exhibiting temporal change as mentioned above. The model allows for selecting between two Gaussian fitness functions that give qualitatively similar results. The strength of selection γ affects the width of the fitness function and its value affects the type of organism that is simulated, with specialists experiencing the strongest selection and generalists the weakest. Thus, the fitness w of individual i is given by:

Method 1 as in (Björklund et al. 2009)

$$wi = 1 - \frac{(zi - \theta t)^2}{\gamma}$$

Method 2 as in (Burger and Lynch 1995)

$$wi = e^{\frac{-(zi - \theta t)^2}{2\gamma^2}}$$

- Set fecundity

The fecundity of the reproductive couple is the sum of the scaled fitness values (*w'i*) of the two parents after considering density dependence effects. The fitness was scaled as in Björklund et al. (2009):

$$w'i = wie^{\psi(1-\frac{N}{K})}$$

where *N* is the population size and *K*, the carrying capacity. The parameter ψ describe the strength of the density dependence effect. The higher the ψ, the stronger is the density dependence effect. Varying the parameter ψ allows simulating fundamentally different population dynamics and therefore different life strategies.

- Run reproduction

Adult individuals mate randomly with others of opposite sex, with replacement only for males (i.e., males can participate in more than one reproductive event). The fecundity of the couple λ is equal to the sum of the scaled fitness of the partners *i,j*

$$\lambda = w'i + w'j$$

Each couple produces a number of offspring randomly drawn from a Poisson distribution with expectancy λ

The process of inheritance of the genetic component a occurs according to two common methods in the literature: implicit or explicit genetics. The user can select the preferred method in the user interface.

Method 1 implicit genetics

In this method, genetics is implicit according to the infinitesimal model of quantitative genetics (Lynch and Walsh 1998), which assumes that quantitative traits are affected by a large number of loci of additive effects. Therefore trait inheritance can be approximated using a normal distribution with mean centered on the arithmetic mean of the two parental trait values, and variance equal to half the additive genetic variance for the trait. The model allows for selecting among three common methods for the modeling of the additive genetic variance: 1) as an input parameter (Reed et al. 2011); 2) population-level (Vincenzi, De Leo, and Bellingeri 2012); or 3) family-level (additive genetic variance of parents) (Björklund et al. 2009). We decided to modify the infinitesimal model as in Vincenzi et al. (2012) in order to account for the decline of additive genetic variance and the new input from mutations. Thus, the variance σG of the distribution is given by

$$\sigma G = \frac{1}{2}(\sigma A + \sigma m M)$$

where σA is the additive genetic variance, σm, the mutational variance, and M, the amplitude or effect size of mutations.

Method 2 explicit genetics

The genetic component a is determined by L unlinked diploid loci of additive effects within and among loci, as in Vincenzi (2014). Thus,

$$a = \sum_{l=1}^{L} nl$$

where nl is the sum of allelic values at locus l. The number of loci L is an input parameter. Each offspring inherit one strain copy or haplotype from each parent. Allele values for each locus of the inherited haplotype are picked randomly from the corresponding parental locus (Recombination). Then, mutations take place with probability μ of mutation per locus. In case that a mutation occurs, its effect is randomly drawn from a normal distribution with zero mean and variance equals to the effect size of mutations, which is an input parameter (Vincenzi 2014). The mean of the distribution of mutation effect size can change according to the percentage of beneficial mutations (input parameter, see below). The assumption of a Gaussian distribution is consistent with analysis of mutation effects (Lynch and Walsh 1998; Martin, Lenormand, and Goodnight 2006).

Method for beneficial mutations

The mean x of the distribution of mutation effect size was given by $x = \varepsilon - y\sqrt{MV}$, where $\varepsilon = 0$ was the Z-score cutting value between deleterious and beneficial mutations. The parameter MV was the variance of the distribution, and y was given by the quantile function of the normal distribution with probability $p = 1 - q$. The parameter q was the desired proportion of beneficial mutation (e.g., 0.25 for 25% scenario of beneficial mutations) (Romero-Mujalli et al. in revision).

The environmental component e of the phenotype is computed as explained above for phenotypic plasticity.

- Adults die

The model considers non-overlapping generations, and therefore, all adults die after the reproduction phase of the model.

- Update phenotype

This function computes (or updates) the phenotype z of individual i as an additive linear combination of its genetic and environmental or phenotypic plasticity components, a and e, respectively. Thus,

$$z = a + e$$

- Check extinction

The model stops if extinction occurs, $N = 0$, before the time limit is reached.

References

Araújo, Cristiano V.M., Cândida Shinn, Matilde Moreira-Santos, Isabel Lopes, Evaldo L.G. Espíndola, and Rui Ribeiro. 2014. “Copper-Driven Avoidance and Mortality in Temperate and Tropical Tadpoles.” *Aquatic Toxicology* 146 (January): 70–75. https://doi.org/10.1016/j.aquatox.2013.10.030.

Ayllón, Daniel, Steven F. Railsback, Simone Vincenzi, Jürgen Groeneveld, Ana Almodóvar, and Volker Grimm. 2016. “InSTREAM-Gen: Modelling Eco-Evolutionary Dynamics of Trout Populations under Anthropogenic Environmental Change.” *Next Generation Ecological Modelling, Concepts, and Theory: Structural Realism, Emergence, and Predictions* 326 (April): 36–53. https://doi.org/10.1016/j.ecolmodel.2015.07.026.

Björklund, Mats, Esa Ranta, Veijo Kaitala, Lars A. Bach, Per Lundberg, and Nils Chr. Stenseth. 2009. “Quantitative Trait Evolution and Environmental Change.” *PLoS ONE* 4 (2): e4521. https://doi.org/10.1371/journal.pone.0004521.

Bridle, Jon R., Jitka Polechová, Masakado Kawata, and Roger K. Butlin. 2010. “Why Is Adaptation Prevented at Ecological Margins? New Insights from Individual-Based Simulations.” *Ecology Letters* 13 (4): 485–94. https://doi.org/10.1111/j.1461-0248.2010.01442.x.

Bürger, R., and C. Krall. 2004. “Quantitative-Genetic Models and Changing Environments.” In *Evolutionary Conservation Biology*, edited by R Ferrière, U. Dieckmann, and D. Couvet, 171–187. Cambridge: Cambridge University Press. doi:10.1017/CBO9780511542022.

Burger, Reinhard, and Michael Lynch. 1995. “Evolution and Extinction in a Changing Environment: A Quantitative-Genetic Analysis.” *Evolution* 49 (1): 151–63. https://doi.org/10.2307/2410301.

Jordan, Percy J., and Lewis E. Deaton. 1999. “Osmotic Regulation and Salinity Tolerance in the Freshwater Snail Pomacea Bridgesi and the Freshwater Clam Lampsilis Teres.” *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 122 (2): 199–205. https://doi.org/10.1016/S1095-6433(98)10167-8.

Kopp, Michael, and Sebastian Matuszewski. 2014. "Rapid Evolution of Quantitative Traits: Theoretical Perspectives." *Evolutionary Applications* 7 (1): 169–91. https://doi.org/10.1111/eva.12127.

Lynch, M., and B. Walsh. 1998. *Genetics and Analysis of Quantitative Traits*. Sinauer. https://books.google.de/books?id=UhCCQgAACAAJ.

Martin, Guillaume, Thomas Lenormand, and C. Goodnight. 2006. "THE FITNESS EFFECT OF MUTATIONS ACROSS ENVIRONMENTS: A SURVEY IN LIGHT OF FITNESS LANDSCAPE MODELS." *Evolution* 60 (12): 2413–27. https://doi.org/10.1554/06-162.1.

Reed, Thomas E., Daniel E. Schindler, Merran J. Hague, David A. Patterson, Eli Meir, Robin S. Waples, and Scott G. Hinch. 2011. "Time to Evolve? Potential Evolutionary Responses of Fraser River Sockeye Salmon to Climate Change and Effects on Persistence." *PLOS ONE* 6 (6): e20380. https://doi.org/10.1371/journal.pone.0020380.

Schwager, Monika, Karin Johst, Florian Jeltsch, Associate Editor: Wolf M. Mooij, and Editor: Michael C. Whitlock. 2006. "Does Red Noise Increase or Decrease Extinction Risk? Single Extreme Events versus Series of Unfavorable Conditions." *The American Naturalist* 167 (6): 879–88. https://doi.org/10.1086/503609.

Solan, Martin, and Nia Whiteley. 2016. *Stressors in the Marine Environment: Physiological and Ecological Responses; Societal Implications*. Oxford, UK: Oxford University Press.

Vincenzi, Simone. 2014. "Extinction Risk and Eco-Evolutionary Dynamics in a Variable Environment with Increasing Frequency of Extreme Events." *Journal of The Royal Society Interface* 11 (97). https://doi.org/10.1098/rsif.2014.0441.

Vincenzi, Simone, Giulio A. De Leo, and Michele Bellingeri. 2012. "Consequences of Extreme Events on Population Persistence and Evolution of a Quantitative Trait." *Ecological Informatics* 8 (March): 20–28. https://doi.org/10.1016/j.ecoinf.2011.12.001.

Appendix 4B

Supporting information to Chapter 4

USER MANUAL

What does this Manual do?

This manual explains how to install and use the user interface of the model PanModel33. The purpose of this model is to understand the potential for local adaptation of populations with different life strategies under scenarios of environmental change. The model was designed for hypothesis testing, theory development and for communication and learning.

The model was designed in such a way that there is no need to modify the code for its operation, unless the user feels confident enough as to extend the model to suit his/her particular needs.

More technical details about the model can be found in the ODD protocol that comes along with this manual.

Table of contents

1 Installation of Netlogo

The first step is to get Netlogo up and running in the computer. Netlogo is a free open source software, very popular for education and research worldwide, that provides a programmable multiagent modeling environment.

To download and install Netlogo visit the following link:

https://ccl.northwestern.edu/netlogo/index.shtml

1.2 Compatibility

Netlogo is compatible with Linux, Windows, and Mac OS, and can run on almost any computer. The link below leads to Netlogo System Requirements

https://ccl.northwestern.edu/netlogo/requirements.html

2 Model versions and description

There are two model versions available to download. The full version takes advantage of the Netlogo *r extension* for the simulation of different scenarios of beneficial mutations. If this feature is not of interest for the user(s), the other simplified version is recommended. The simplified version uses Netlogo resources only (no need of additional programs and complications).

To use the full version of the model, please follow the steps on the link below. This link explains how to set up the Netlogo r extension which is important before using the model (search for “installing r”, and “configuring the r extension”). Otherwise, it will not work properly.

https://ccl.northwestern.edu/netlogo/docs/r.html

2.1 Using the model user interface

If you are using Netlogo for the first time, it is strongly recommended to get familiar with the basics regarding the operation of the user interface of the software. For example, it is important to understand what the different bottoms do (setup, go and forever bottoms), as well as how to change parameter values using sliders, choosers and input boxes. Netlogo provides a friendly tutorial on their webpage for the learning of the user interface and more (link below)

https://ccl.northwestern.edu/netlogo/docs/tutorial1.html

2.2 Plots

The user interface of the model contains the following plots that display output data in real simulation time (Fig 1):

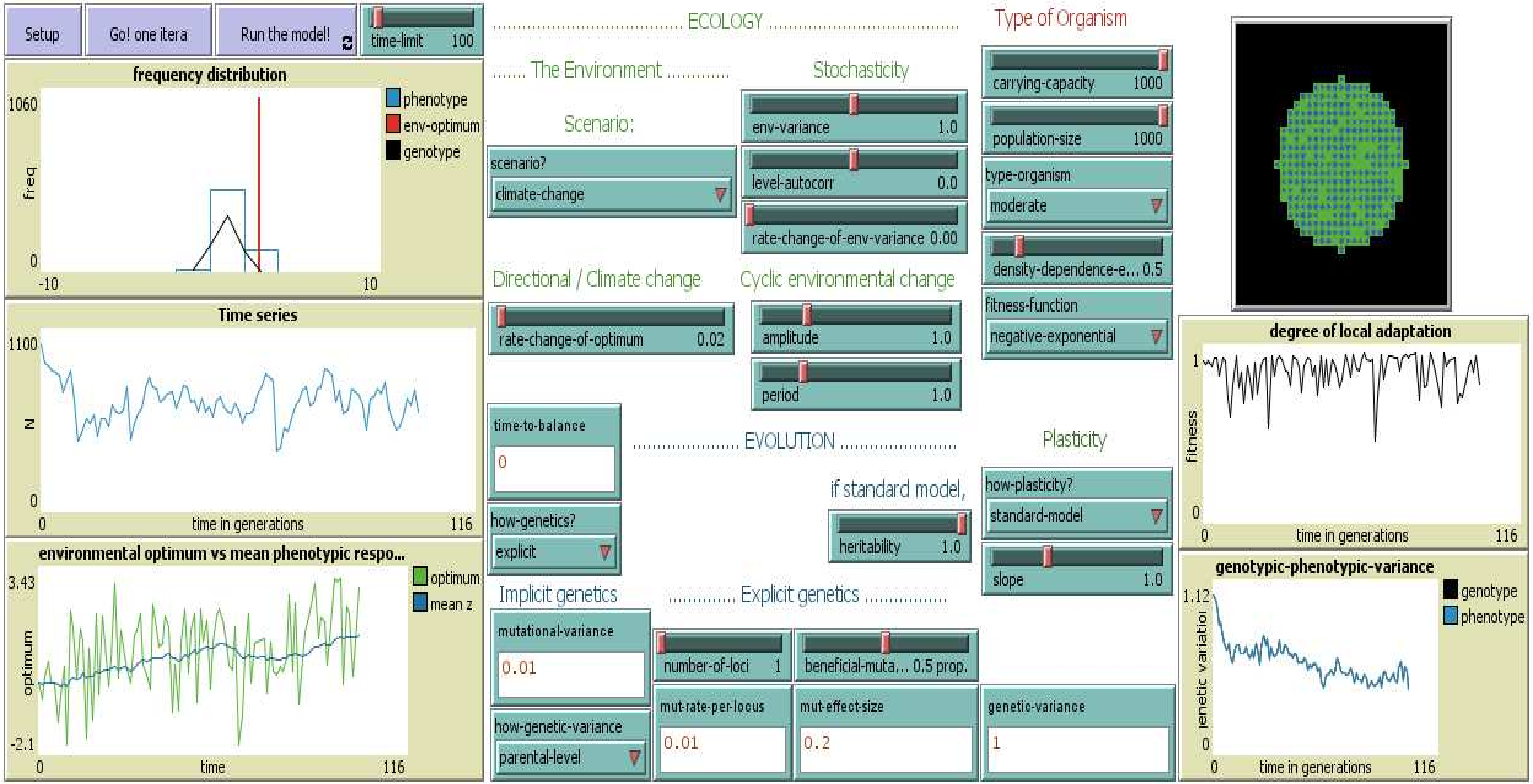
- *Frequency distribution: display the phenotypic (blue) and genotypic (black) frequency distributions in the population. It also shows the optimum phenotype as given by the environment (red vertical line).*
- *Time series: this plot monitors the population size.*
- *Genotypic-phenotypic-variance: keeps track of the actual genetic and phenotypic variances in the population.*
- *Degree of local adaptation: monitors how fit the population is to the environment (fitness proxy).*
- *Environmental optimum vs mean phenotypic response: display how far is the population mean phenotype from the optimum as given by the environment.*

2.3 Bottoms

The bottoms (top left) allow to set up the experiment, and run the model for only one iteration, or until either, the ending condition of time-limit is met, or extinction occurs.

2.4 The Ecology and Evolution modules

The input parameters of the eco-evolutionary model that the user can modify are grouped into two modules: the ecological module (Ecology), and the evolutionary module (Evolution). The Ecology module governs the scenario of environment and the type of organism, while the Evolution module, the underlying genetics, and plasticity. The genetics is further split into explicit or implicit, depending on whether the chromosomes, loci, mutation rates and other genomic properties are explicitly simulated or not.



time-limit 100

scenario? climate-change

env-variance 1.0

level-autocorr 0.0

rate-change-of-env-variance 0.00

rate-change-of-optimum 0.02

amplitude 1.0

period 1.0

carrying-capacity 1000

population-size 1000

type-organism moderate

density-dependence-e... 0.5

fitness-function negative-exponential

time-to-balance 0

how-genetics? explicit

heritability 1.0

how-plasticity? standard-model

slope 1.0

mutational-variance 0.01

how-genetic-variance parental-level

number-of-loci 1

beneficial-muta... 0.5 prop.

mut-rate-per-locus 0.01

mut-effect-size 0.2

genetic-variance 1

Fig 1 Picture of the graphical user interface (GUI) of the eco-evolutionary model.

3 Description of adjustable parameters of the GUI, their description and range of values.

Module		Parameter name	Description	Range	default
Ecology	Environmental scenario	scenario?	whether climate change or cyclic environment		Climate-change
		rate-change-of-optimum	rate of change of environmental optimum per time step (climate change only)	[0.00; 1.00]	0.02
		amplitude	amplitude of the wave (only for cyclic environmental scenario)	[0.0; 4.0]	1.0
		period	period of the wave (only for cyclic environmental scenario)	[0.0; 4.0]	1.0
		env-variance	the variance of the stochastic environment	[0.0; 2.0]	1.0
		rate-change-of-env-variance	rate at which the environmental variance change per time step	[0.00; 0.10]	0
		level-autocorr	the level of autocorrelation, for simulating colored stochastic noise: white, blue or red noise	(-1.0; 1.0)	0 (white noise)
	Type of organism	carrying capacity	the carrying capacity of the local environment (in number of individuals)	[10; 1000]	1000
		population-size	initial number of individuals in the population	[10; 1000]	1000
		type-organism	level of specialization of the simulated organism	[specialist; moderate; generalist]	moderate
		density-dependence-effect	whether the simulated organism is an *r* or *K* strategist, depending on whether the density dependence effect is strong or weak	[0; 3.0]	0.5 (weak)
		fitness-function	two possible methods, both assuming a bell-shaped fitness function	[Bjoerklund2009; negative-exponential]	negative-exponential
Evolution		time-to-balance	the number of time steps before the actual scenario of environment starts	≥ 0	0
		how-plasticity?	Selection among different methods for phenotypic plasticity. For the method standard-model, its contribution to phenotypic variance depends on the value of heritability	standard-model, random, linear-RN, adaptive-sinusoidal, adaptive-logistic	standard-model
		slope	degree of plasticity	[0.5; 2.0]	1.0
		heritability	the value for trait heritability. A value of one, means that the correlation genotype-phenotype is one (*i.e.*, no plasticity or environmental effect). Only works for standard model (see how-plasticity)	[0.01; 1.00]	1.0
		genetic-variance	initial genetic variance in the population	≥ 0	1
		how-genetic-variance	specifies the method for simulating the dynamics of the genetic variance (works only for the standard model)	[parameter; parental-level; population-level]	parental-level
		how-genetics?	set the method for simulating genetics	[implicit ; explicit]	explicit
	Implicit genetics	mutational-variance	the amount of genetic variance contributed by mutations	≥ 0	0.01
	Explicit genetics	number-of-loci	the number of loci affecting the fitness-related trait (evolving trait)	[1 ; 50]	1
		mut-rate-per-locus	probability of mutation per locus	≥ 0	$1x10^{-3}$
		mut-effect-size	the variance of the fitness effect-size of mutations. The model assumes a Gaussian distribution of effect-size	≥ 0	0.2
		beneficial-mutations	set the percentage of beneficial mutations (affect the distribution of mutation effects accordingly)	[0.1; 0.9]	0.5

Chapter 5

General Discussion

CHAPTER 5

General Discussion

The Universe / Nature inspires all questions and contains all answers

Always think the world as bigger, so you can give room for surprises

This dissertation had two main objectives: (1) to perform a review on the state of the art of eco-evolutionary individual-based models (IBMs), and (2) to study the effect and limits of evolutionary mechanisms on the local adaptation ability of populations with different life strategy experiencing scenarios of climate change. In this chapter I will recall some of the main results from the previous chapters in order to answer the main research questions that were presented in the introduction. Therefore, I will divide my findings again in blocks for the discussion, highlighting how they connect to each other and contribute to knowledge. Though some repetition will be inevitable, in this chapter I will focus more on the products and consequences of these findings, what did I learn, shortcomings, and avenues for future work.

5.1 Objective 1: State of the art and knowledge gaps of eco-evolutionary IBMs

According to the literature review (Chapter 2), the topic of phenotypic plasticity represents a knowledge gap in eco-evolutionary IBMs. The most common approach for the modeling of phenotypic plasticity was to assume that the environment induces a random effect on the development of the phenotypic trait (*i.e.*, the random noise approach); and for its evolution, linear reaction norms. In the absent of costs, linear reaction norms can lead to the evolution of perfect plasticity (Lande 2009; Lande 2014), which has not been empirically observed. However, according to the empirical evidence, costs to plasticity seem to be negligible (Murren et al. 2015). In addition to costs, plasticity must also have limits (DeWitt et al. 1998; Pigliucci 2005). Eco-evolutionary IBMs explicitly accounting for limits to phenotypic plasticity were not found. In fact, limits to plasticity have generally received little attention in the literature (Murren et al. 2015). Thus, the outcome of this review motivated me to start exploring the effect of explicit limits to phenotypic plasticity on the ability for local adaptation of populations experiencing novel local environmental conditions (Chapter 4)

Most (if not all) the reviewed literature implementing the random noise approach does not consider it as part of phenotypic plasticity, despite it fits well most of the proposed definitions for phenotypic plasticity. West-Eberhard (2003) proposes random developmental noise as a form of plasticity that cannot be related to a specific measured environmental variable. In addition, what is regarded as random variation when measuring a given phenotypic character could be due to developmental instability and micro-environmental fluctuations during its ontogeny (*i.e.*, plasticity occurring at the microlevel – of cells – during development) (Futuyma et al. 2005; Kopp and Matuszewski 2014). In fact, generating random phenotypic diversity at the individual level can even be of advantage in some situations (see results in Chapter 4, Donaldson-Matasci et al. 2013).

An additional avenue for future research using eco-evolutionary IBMs is the simultaneous consideration of evolutionary dynamics in relevant traits governing the potential responses of organisms experiencing environmental change (*i.e.*, local genetic adaptation, plasticity and dispersal). This thesis focused on local adaptation only. However, I programmed the code thinking in a future extension of the model to simulate dispersal in heterogeneous landscapes. My idea was to prepare the model to study evolutionary dynamics in relevant traits governing the population responses to environmental change mentioned above.

Personally, this literature review greatly helped me to quickly find methods that could reflect the joint ideas I had together with my PhD colleagues of the research school “Adaptive Evolutionary Responses to Rapid Climate Change” at the University of Potsdam. This resulted in the eco-evolutionary modeling tool I developed and used for the research topics shown in Chapters 3 and 4, and that will be release along the publication of the manuscript presented in Chapter 4.

5.2 Objective 2a: on the evolution of the mutation rate in a population of a sexual species experiencing climate change

Since mutations are the ultimate source of genetic variation, the question of whether the mutation rate can evolve to elevated values and increase evolvability of populations has arisen repeatedly in the literature (Leigh 1970; Johnson 1999; Shaver et al. 2002; Clark et al. 2011; Martincorena and Luscombe 2013; Cobben et al. 2017). A recent study found elevated mutation rates to evolve in a sexual species and that this can promote its invasion speed and adaptation to novel environmental conditions (Cobben et al. 2017). In their model, this was possible through induced linkage disequilibrium between the dispersal locus and the mutator locus due to spatial sorting and iterated founder event (Cobben et al. 2017). Motivated by their findings, I investigated whether the mutation rate could also evolve and enhance the ability for local adaptation of a population of a sexual species experiencing scenarios of climate change. My results show that the mutation rate can evolve to elevated values and enhance the population's ability to sustain climate change under scenarios of complete linkage between the adaptation locus and the mutator locus, and when unlinked, only when the rate of change was fastest and beneficial mutations were as high as 50%. In my model, each individual in the population had an adaptation locus coding for its preferred environmental condition (*e.g.*, optimal temperature). The simulation of scenarios of linkage disequilibrium was important, because it has been shown to affect the evolution of the mutation rate (Leigh 1970; Johnson 1999). Thus, my hypothesis (see Chapter 1) was confirmed, except for the scenario of 50% probability of beneficial mutations. Under this scenario, most of the mutations are expected to be neutral, but deleterious and beneficial mutations are assumed to occur with equal likelihood, which contradicts empirical evidence on the distributions of fitness effects (Martin et al. 2006; Eyre-Walker and Keightley 2007). Evidence suggests that most mutations are deleterious, some are neutral, and few beneficial (Drake et al. 1998), with beneficial mutations displaying an exponential decay (Eyre-Walker and Keightley 2007). Therefore, the hypothesis was not met for a rather unrealistic scenario.

According to my review (Chapter 2), most eco-evolutionary IBMs implement mutations effects according to the scenario of 50% beneficial mutations explained above. My research proposes an alternative method for the simulation of mutations effects based on the concept of slightly deleterious mutations (Ohta 1973; Eyre-Walker et al. 2002). This assumption can impact modeling outcomes when investigating the potential for evolutionary rescue and the relative importance of phenotypic plasticity (Chapter 4). Future work should focus on studying these two topics under more realistic assumption of beneficial mutations.

In a sexual species, scenarios of complete linkage can occur if the mutator locus (*e.g.*, a locus encoding the DNA polymerase) is somehow linked to loci coding for traits under selection (here, the adaptation locus). This is plausible, if they are in close proximity, in the same chromosome. However, in these species most traits under selection are expected to occur far away in the genome – or in a different chromosome – with respect to the mutator locus (unlinked scenario). Therefore, my results suggest that it is unlikely that the mutation rate will evolve and promote evolvability in a sexual species experiencing climate change. The mutation rate is then expected to remain low, limited by costs of replication fidelity or by the drift limit, as already suggested in the literature (Lynch 2011). In contrast, my results on the complete linkage scenario suggest that the mutation rate can evolve to elevated values in an asexual species experiencing climate change scenarios. This result agrees with previous theoretical and experimental studies investigating the evolution of the mutation rate in asexual organisms under changing environmental conditions (Leigh 1970; Shaver et al. 2002).

An interesting model observation was that the evolutionary trajectory of the mutation rate was the same, independently of the form of environmental fluctuations or noise color. This match observations of no systematic variation in the mutation rate among organisms experiencing different habitats or climatic conditions (Martincorena and Luscombe 2013).

Overall, my results discard that the mutation rate will evolve and enhance evolvability of sexual species, though it might for asexual organisms, especially for unicellular ones. It is important to mention that elevated mutation rates in multicellular organisms, under the assumption of a mutator locus, may compromise the integrity and function of their soma and, hence, their survival. Sexual species experiencing climate change scenarios will rely on standing genetic variation and phenotypic plasticity for their ability of local adaptation, particularly when fecundity is low and population size, small. Chapter 4 (and the discussion below) complements these findings and adds on the role of phenotypic plasticity in these populations, and in populations with other life strategies, experiencing scenarios of climate change.

The topic of Chapter 3 helped me to get a deeper understanding of the action and limitations of genetic mechanisms, and of their potential promoting evolutionary rescue of populations experiencing environmental change. In addition, I also realized that the distribution of mutation fitness effects still represents a knowledge gap. Perhaps (speculation warned!) its tendency to slightly deleterious mutations may be related to the fact that the trait is already close to a local optimum, and any departure (be it, an increase or decrease in trait value) will more likely add to deleterious effects.

5.3 Objective 2b: on the relative importance of forms of plasticity for populations with different life strategy experiencing climate change scenarios

According to literature, theoretical models predict that selection will favor adaptive phenotypic plasticity in variable environmental conditions when environmental cues are reliable, costs negligible, and when selection favors different phenotypes in each environment (Ghalambor et al. 2007; Hendry 2016a). Most studies on phenotypic plasticity has focused on the adaptive nature of plasticity (Ghalambor et al. 2007; Lande 2009; Chevin et al. 2010; Lande 2014), though it can also be non-adaptive (Ghalambor et al. 2007; Donaldson-Matasci et al. 2013; Hendry 2016a). In this study, I add to this knowledge and show that, even when environmental cues are reliable, adaptive phenotypic plasticity can hinder evolution and compromise population persistence. This occurs when environmental fluctuations are characterized by high frequency changes typical of bluish climates. Under these conditions (only blue stochastic noise, no climate change), populations relying on adaptive plasticity will experience amplified phenotype-environment mismatches in the long run due to the negative autocorrelation of the climatic variable. Via the process of genetic accommodation[1], genes will follow in the direction of the adaptive plastic response. Subsequently, because of the negative autocorrelation, future generations will experience environmental conditions even beyond their capabilities for adaptive plasticity, which then can lead to population decline and increased risk of extinction. My model assumes non-overlapping generations. Future work should investigate whether this observation still holds for species with overlapping generations under bluish climate conditions. Similar results have been found in models assuming negative correlation among the environmental cues and the phenotypic optimum as given by the environment (Ashander et al. 2016). When cues are not reliable, adaptive phenotypic plasticity isn't favor either. Thus, under these types of variable climatic conditions, selection will favor other forms of phenotypic plasticity: in my model, random noise (also called random phenotypic diversity, Donaldson-Matasci et al. 2013). In my model, random noise was considered non-adaptive phenotypic plasticity. It was simulated as a random effect on the development of the phenotypic trait. Under this plasticity scenario, the trait developed randomly in any direction with respect to the environmental optimum. This form of random phenotypic diversity can be of advantage when environmental conditions are unpredictable (Reed et al. 2010) or cues unreliable (Donaldson-Matasci et al. 2013), for example, droughts, floods, and peaks of food availability. It has been mainly related to timing traits (Visser et al. 2012; McAllan et al. 2012) and reported as a common strategy among plant species inhabiting arid habitats (Philippi 1993). According to my results, this form of non-adaptive phenotypic plasticity was particularly advantageous promoting population persistence under negatively autocorrelated (blue noise) and uncorrelated (white noise) environmental conditions, and when the rate of change was intermediate, slower, or absent.

Most fluctuations of climatic variables are characterized by a white or red-brown spectra (Vasseur and Yodzis 2004). However, over the last century the spectra of temperature climate variables on most continents has become bluer (García-Carreras and Reuman 2011). Under such new bluish climates, my findings suggest that populations of organisms relying on adaptive phenotypic plasticity will be vulnerable. Unless they can either, change their plastic strategy, or reduce their reliance on

---

[1] The process of genetic accommodation occurs when phenotypic variants that are environmentally induced, become genetically determined by natural selection (West-Eberhard 2003; Schlichting and Wund 2014)

adaptive phenotypic plasticity. Therefore, regarding the recursive question in the literature, whether adaptive phenotypic plasticity promotes or hinders evolution, my findings show environmental conditions in which adaptive phenotypic plasticity can hinder adaptive evolution.

In addition, and in line with the literature, my findings show that adaptive phenotypic plasticity can also promote evolution. This effect is particularly relevant when a population is experiencing fluctuations characterized by positive autocorrelation of the climatic variable, typical of reddish climates. Thus, adaptive phenotypic plasticity can decrease the extinction risk of populations inhabiting reddish climates, which is expected to be high in the absent of plasticity (Mustin et al. 2013). Furthermore, I found that adaptive phenotypic plasticity promotes population persistence for a larger range of forms of environmental fluctuations (or a broader spectrum of noise color) in comparison to non-adaptive plasticity and genetic determinism, when the population is experiencing intermediate to rapid rates of environmental change. Thus, my model predicts that populations experiencing local environmental change (*e.g.*, due to climate change) and, probably, those populations located at the front of the expanding range, will benefit from adaptive phenotypic plasticity. This is, because in both scenarios, populations will be experiencing a directional trend in the phenotypic optimum as given by the environment (*e.g.*, towards tolerating colder or warmer climate conditions).

In this sense, the hypothesis 1 of this research topic is not met. When organisms can respond in the direction of the stochastic optimum through adaptive phenotypic plasticity, this can hinder evolution of the population and compromise its persistence under bluish environmental conditions. In contrast, adaptive phenotypic plasticity can buffer fitness losses and increase persistence of populations experiencing reddish climates (in comparison to non-adaptive plasticity and genetic determinism), and for a broader spectrum of noise color when the rate of environmental change is intermediate to rapid.

On the other hand, my findings show that the relative importance of either form of phenotypic plasticity depends on the life strategy. To my knowledge this field has been understudied in the literature. In my model, life strategies had contrasting intrinsic population dynamics, and differed in the number of offspring that reproductive couples could produce (fecundity). My results show that, if populations of sexual species differing in their life strategy happen to experience similar or equivalent rates of directional climate change and forms of environmental stochasticity, those with limited fecundity will rely more in any adaptive form of phenotypic plasticity to cope with environmental conditions (except under bluish climates!). In contrast, populations of species with higher fecundity will be able to rely on non-adaptive phenotypic plasticity and evolutionary rescue only. Adaptive phenotypic plasticity was particularly important for life strategies with an expected maximum fecundity of $\lambda \leq 4$ individuals. In my model, this parameter was used to draw the number of offspring from a Poisson distribution. These simulated life strategies of limited fecundity resemble well mammal (especially large mammal species, including humans) and bird species. Since adaptive forms of plasticity might be costlier (especially if it is flexible), my model predicts that populations of species with relatively low fecundity will experience stronger selection for the developing of adaptive forms of plasticity (*e.g.*, cognitive abilities), than populations with higher fecundity. This will be particularly favored when these species are inhabiting reddish climates, or – for broader climate conditions – when experiencing directional environmental change either, in their local habitat, or as they move into new habitats. It is important to consider that, for the model, life strategies differ mainly in their intrinsic population dynamics and fecundity. Thus, other factors, for example, longevity in plants, may impose selection towards forms of adaptive plasticity as well (Borges 2008).

Thus, the hypothesis 2 of this research is met. Those populations in which individuals are limited to produce relatively few offspring will rely more in phenotypic plasticity (particularly, adaptive forms of plasticity) than those with individuals with higher fecundity. These results (Chapter 4) complement the findings in Chapter 3 and show how phenotypic plasticity can promote local adaptation of populations when factors boosting a genetic response are somehow constrained (*e.g.*, when fecundity is low, and populations are small and isolated).

Personally, this research (Chapter 4) made me appreciate the importance of considering different forms of fluctuations or stochastic noise color for the understanding of population persistence. Additionally, it provided me with the opportunity to materialize own ideas for the modeling of forms of adaptive phenotypic plasticity.

5.4 Brief considerations on the implementation of adaptive phenotypic plasticity

For my model, I designed a novel method for phenotypic plasticity that impose limits to the plastic response. This method assumes plasticity to be constructive (*sensu* Laland et al. 2015), to rely on feedback from the environment, and to act in the direction of the environmental optimum (adaptive). It assumes that organisms can sense their environment and react accordingly. Thus, the method considers the bidirectionality of interactions (van Gestel and Weissing 2016). In this method, organisms are active agents, instead of passive, which seems to be in line with some developmental mechanisms (*e.g.*, vasculogenesis, Gerhart and Kirschner 2007), and many physiological and behavioral traits (*e.g.*, learning). It can mechanistically be linked to epigenetic mechanisms, and neural networks. Also, it can be easily implemented for the modelling of phenotypic plasticity on constant and flexible characters. Furthermore, it allows organisms to still respond adaptively – within its limits – to novel environmental conditions, and the process of genetic accommodation is observed without further assumptions (*e.g.*, costs to plasticity). Additionally, it fits well the theory of facilitated variation proposed by Gerhart and Kirschner (2007).

The assumption of constructive development leads to stable functioning of the phenotype (close to the optimum) regardless of variation at the genetic level (*developmental canalization*, Posadas and Carthew 2014). This feature implies robustness, redundancy, and adaptability of regulatory networks at the microlevel, and thus, can act as a mechanism that maintain genetic variation, potentially increasing evolvability (Gerhart and Kirschner 2007; van Gestel and Weissing 2016). An additional implication is that the phenotypic variance, sometimes, will be smaller than the genetic variance in the population. A question that arises is whether this feature can affect the interpretation of heritability.

In this method, depending on the assumption of limits to plasticity, cryptic variation may arise when plasticity is pushed towards its limits. Therefore, in such scenario, most of the cryptic variation will be maladaptive. Further work is needed to study the validity of the assumptions and predictions of this method.

So far, this method is phenomenological. However, here I would like to propose an avenue for future work into a more mechanistic understanding of this form of plasticity and its limits. I propose to take a mechanistic agent/individual-based model approach of explicit genetics (Grimm and Railsback 2005; Romero-Mujalli et al. 2018), and to focus on epigenetics effects on the plasticity of a quantitative trait like body size. For example, epigenetics markers silencing or activating a finite number of loci of additive effects can affect variation of the quantitative trait. In this case, silencing could make body size smaller. Furthermore, because the number of loci affecting the trait are finite, this will already impose limits to plasticity, which has received little attention in the literature (Murren et al. 2015). The presence of epigenetic modifications may also confer redundancy and robustness to regulatory networks at the microscopic level (Gerhart and Kirschner 2007; Posadas and Carthew 2014; van Gestel and Weissing 2016). Depending on the time period of developmental sensitivity, and the length (complexity) of the coding genome sequence, memory of epigenetic markers (non-genetic inheritance) may arise.

5.5 Caveats, limitations, shortcomings:

Results reported in Chapter 3 are valid under the assumption of a mutator locus (*e.g.*, coding for DNA polymerase), which is in line with most research on the evolution of the mutation rate (Leigh 1970; Gillespie 1981; Cobben et al. 2017). However, the consideration of additional mechanisms affecting the mutation rate (*e.g.*, epigenetic mechanisms, Odegard and Schatz 2006; Martincorena and Luscombe 2013) can affect the results as reported in this study.

It is important to mention that the findings reported in Chapter 4 for non-adaptive plasticity may not hold if the variance in the phenotypic trait due to this form of plasticity is different from the variance of the stochastic fluctuations of the climate variable imposing selection. My implementation is based on previous studies using the random noise approach (Burger and Lynch 1995; Bürger and Krall 2004; Kopp and Matuszewski 2014; Vincenzi 2014). Yet, this assumption should be taken with cautious, particularly when investigating the effects of climate change on the environmental variance (*e.g.*, climate change scenarios with increasing environmental variance, Vincenzi 2014). A related question that follows is: what mechanisms govern the magnitude of such a random plastic response? Can this somehow match the environmental variance?

Furthermore, the model, as in any other IBMs of explicit genetics (Romero-Mujalli et al. 2018), assumes 50% beneficial mutations which was shown in Chapter 3 to be unrealistic. It also assumes non-overlapping generations. Thus, time is measured in generations, which is typical of models focused on evolutionary mechanisms (Burger and Lynch 1995; Kopp and Matuszewski 2014). However, this assumption can be critical for the study of phenotypic plasticity on constant and flexible characters.

5.6 Future work, road ahead

“when we believed to have all answers, all questions suddenly changed” (M. Benedetti)

Hopefully, this dissertation opens many doors for future research, especially considering that many of the features that are currently implemented in the modeling tool have not been explored yet. For instance, in addition to the environmental scenarios studied in this dissertation, the model also includes seasonal environmental changes (with or without stochastic noise), and scenarios of increasing variance due to climate change. In this chapter, I have already proposed topics for future research derived from my work, which, I hope, can inspire future Master and PhD projects. Below, I comment on some personal ideas (wishes) for the continuation of the work started with this dissertation.

The code of the eco-evolutionary modeling tool is already preconditioned to be extended to account for dispersal in heterogeneous landscapes. Such an extension would open the opportunity to simulate evolutionary dynamics in relevant traits governing organisms’ responses to environmental change, which (according to Chapter 2) has not been done yet.

The model can be used for teaching. It can be useful for students to *learn by doing* basic concepts in Evolutionary Biology and Ecology. The user graphic interface includes many plots that record the eco-evolutionary dynamics in real time, is user friendly (or at least I hope so), and the model can be used without the need of visiting the code. In fact, this modeling tool was successfully tested and used by students of the University of Potsdam during a lecture that I designed and taught in the summer semester 2017.

Finally, this modeling tool may offer an opportunity for collaboration with other larger projects aiming at understanding eco-evolutionary dynamics and species responses to environmental change. For example, the BioMove project at the University of Potsdam, and RESPONSE at the University of Greifswald.

5.7 Conclusions

The main take-home message of this dissertation is that populations of sexual species (particularly those isolated and with low fecundity) will rely mainly on *standing genetic variation* and phenotypic plasticity for local adaptation. Elevated mutation rates are unlikely to evolve to elevated rates and promote evolutionary rescue in these species. Thus, the current paradigm is robust under the assumption of a mutator locus. Population of species with relatively slow growth rate (*e.g.*, large mammals) – especially those of small size – are the most vulnerable, particularly if their plasticity is limited (*i.e.*, specialist species). Whenever organisms from these populations are capable of adaptive plasticity, they can buffer fitness losses in reddish climatic conditions, and while they move into new habitats. Likewise, whenever they can adjust their plastic response (*e.g.*, into bed-hedging strategy) they will cope with bluish environmental conditions as well. In contrast, life strategies of high fecundity can rely on non-adaptive plasticity and evolutionary rescue for their local adaptation to novel environmental conditions, unless the rate of change is too rapid. A recommended management measure is to provide populations of organisms with opportunities to move and follow their preferred niche, and exchange migrants, especially in bluish and reddish climatic conditions, when the rate of change is slow, or for any environmental conditions when the level of stress (rate of change) is relatively high.

6 References

Ashander J, Chevin L-M, Baskett ML (2016) Predicting evolutionary rescue via evolving plasticity in stochastic environments. Proc R Soc B Biol Sci 283:20161690. doi: 10.1098/rspb.2016.1690

Beckerman AP, Childs DZ, Bergland AO (2016) Eco-evolutionary Biology: Feeding and Feedback Loops. Curr Biol 26:161–164. doi: https://doi.org/10.1016/j.cub.2016.01.013

Bell G (2013) Evolutionary rescue and the limits of adaptation. Philos Trans R Soc B Biol Sci 368: doi: 10.1098/rstb.2012.0080

Björklund M, Ranta E, Kaitala V, Bach LA, Lundberg P, Stenseth NC (2009) Quantitative Trait Evolution and Environmental Change. PLoS ONE 4:e4521. doi: 10.1371/journal.pone.0004521

Boag PT, Grant PR (1981) Intense Natural Selection in a Population of Darwin's Finches (Geospizinae) in the Galápagos. Science 214:82. doi: 10.1126/science.214.4516.82

Borges RM (2008) Plasticity comparisons between plants and animals: Concepts and mechanisms. Plant Signal Behav 3:367–375.

Bulmer MG (1971) The Effect of Selection on Genetic Variability. Am Nat 105:201–211. doi: 10.1086/282718

Bürger R, Krall C (2004) Quantitative-Genetic Models and Changing Environments. In: Ferrière R, Dieckmann U, Couvet D (eds) Evolutionary Conservation Biology. Cambridge University Press, Cambridge, pp 171–187

Burger R, Lynch M (1995) Evolution and Extinction in a Changing Environment: A Quantitative-Genetic Analysis. Evolution 49:151–163. doi: 10.2307/2410301

Bush A, Mokany K, Catullo R, Hoffmann A, Kellermann V, Sgrò C, McEvey S, Ferrier S, Coulson T (2016) Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecol Lett 19:1468–1478. doi: 10.1111/ele.12696

Carroll SP, Hendry AP, Reznick DN, Fox CW (2007) Evolution on ecological time-scales. Funct Ecol 21:387–393. doi: 10.1111/j.1365-2435.2007.01289.x

Chevin L-M, Lande R, Mace GM (2010) Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. PLoS Biol 8:e1000357. doi: 10.1371/journal.pbio.1000357

Clark JR, Daines SJ, Lenton TM, Watson AJ, Williams HTP (2011) Individual-based modelling of adaptation in marine microbial populations using genetically defined physiological parameters. Ecol Model 222:3823–3837. doi: 10.1016/j.ecolmodel.2011.10.001

Cobben MMP, Mitesser O, Kubisch A (2017) Evolving mutation rate advances the invasion speed of a sexual species. BMC Evol Biol 17:150. doi: 10.1186/s12862-017-0998-8

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. Trends Ecol Evol 13:77–81. doi: 10.1016/S0169-5347(97)01274-3

Donaldson-Matasci MC, Bergstrom CT, Lachmann M (2013) When Unreliable Cues Are Good Enough. Am Nat 182:313–327. doi: 10.1086/671161

Downing K (1998) Using evolutionary computational techniques in environmental modelling. Environ Model Softw 13:519–528. doi: 10.1016/S1364-8152(98)00050-4

Drake JW, Charlesworth B, Charlesworth D, Crow JF (1998) Rates of Spontaneous Mutation. Genetics 148:1667.

Dunlop ES, Heino M, Dieckmann U (2009) Eco-genetic modeling of contemporary life-history evolution. Ecol Appl 19:1815–1834. doi: 10.1890/08-1404.1

Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu Rev Ecol Evol Syst 40:677–697. doi: 10.1146/annurev.ecolsys.110308.120159

Ergon T, Ergon R (2016) When three traits make a line: evolution of phenotypic plasticity and genetic assimilation through linear reaction norms in stochastic environments. J Evol Biol 30:486–500. doi: 10.1111/jeb.13003

Eyre-Walker A, Keightley PD (2007) The distribution of fitness effects of new mutations. Nat Rev Genet 8:610–618. doi: 10.1038/nrg2146

Eyre-Walker A, Keightley PD, Smith NGC, Gaffney D (2002) Quantifying the Slightly Deleterious Mutation Model of Molecular Evolution. Mol Biol Evol 19:2142–2149. doi: 10.1093/oxfordjournals.molbev.a004039

Ford EB (1975) Ecological Genetics. In: Ford EB (ed) Ecological Genetics. Springer Netherlands, Dordrecht, pp 1–11

Franks SJ, Weber JJ, Aitken SN (2014) Evolutionary and plastic responses to climate change in terrestrial plant populations. Evol Appl 7:123–139. doi: 10.1111/eva.12112

Fussmann GF, Ellner SP, Hairston NG (2003) Evolution as a critical component of plankton dynamics. Proc R Soc B 270:1015–1022. doi: 10.1098/rspb.2003.2335

Fussmann GF, Loreau M, Abrams PA (2007) Eco-evolutionary dynamics of communities and ecosystems. Funct Ecol 21:465–477. doi: 10.1111/j.1365-2435.2007.01275.x

Futuyma DJ, Edwards SV, True JR (2005) Evolution. Sinauer Associates

Galloway LF, Etterson JR (2007) Transgenerational Plasticity Is Adaptive in the Wild. Science 318:1134. doi: 10.1126/science.1148766

García-Carreras B, Reuman DC (2011) An empirical link between the spectral colour of climate and the spectral colour of field populations in the context of climate change. J Anim Ecol 80:1042–1048. doi: 10.1111/j.1365-2656.2011.01833.x

Gerhart J, Kirschner M (2007) The theory of facilitated variation. Proc Natl Acad Sci 104:8582. doi: 10.1073/pnas.0701035104

Ghalambor CK, Mckay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407. doi: 10.1111/j.1365-2435.2007.01283.x

Gillespie JH (1981) Mutation modification in a random environment. Evolution 35:468–476. doi: 10.1111/j.1558-5646.1981.tb04910.x

Gonzalez A, Ronce O, Ferriere R, Hochberg ME (2013) Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. Philos Trans R Soc B Biol Sci 368:20120404. doi: 10.1098/rstb.2012.0404

Grimm V, Railsback SF (2005) Individual-based Modeling and Ecology. Princeton University Press

Heino M, Ripa J, Kaitala V (2000) Extinction risk under coloured environmental noise. Ecography 23:177–184. doi: 10.1111/j.1600-0587.2000.tb00273.x

Hendry AP (2016a) Key Questions on the Role of Phenotypic Plasticity in Eco-Evolutionary Dynamics. J Hered 107:25–41. doi: 10.1093/jhered/esv060

Hendry AP (2016b) Eco-evolutionary Dynamics. Princeton University Press

Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in long–distance migrants, delays in short–distance migrants. Proc R Soc Lond B Biol Sci 270:1467. doi: 10.1098/rspb.2003.2394

Johnson T (1999) Beneficial mutations, hitchhiking and the evolution of mutation rates in sexual populations. Genetics 151:1621–1631.

Klauschies T, Coutinho RM, Gaedke U (2018) A beta distribution-based moment closure enhances the reliability of trait-based aggregate models for natural populations and communities. Ecol Model 381:46–77. doi: https://doi.org/10.1016/j.ecolmodel.2018.02.001

Kopp M, Matuszewski S (2014) Rapid evolution of quantitative traits: theoretical perspectives. Evol Appl 7:169–191. doi: 10.1111/eva.12127

Lakovic M, Mitesser O, Hovestadt T (2017) Mating timing, dispersal and local adaptation in patchy environments. Oikos 126:1804–1814. doi: 10.1111/oik.04369

Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. Proc R Soc B 282:20151019. doi: 10.1098/rspb.2015.1019

Lande R (2014) Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. J Evol Biol 27:866–875. doi: 10.1111/jeb.12360

Lande R (2009) Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. J Evol Biol 22:1435–1446. doi: 10.1111/j.1420-9101.2009.01754.x

Leigh EG (1970) Natural Selection and Mutability. Am Nat 104:301–305.

Lohbeck KT, Riebesell U, Reusch TBH (2012) Adaptive evolution of a key phytoplankton species to ocean acidification. Nat Geosci 5:346–351. doi: 10.1038/ngeo1441

Lynch M (2011) The Lower Bound to the Evolution of Mutation Rates. Genome Biol Evol 3:1107–1118. doi: 10.1093/gbe/evr066

Lynch M, Walsh B (1998) Genetics and Analysis of Quantitative Traits. Sinauer, Sunderland, MA

Marais G, Charlesworth B (2003) Genome Evolution: Recombination Speeds Up Adaptive Evolution. Curr Biol 13:R68–R70. doi: https://doi.org/10.1016/S0960-9822(02)01432-X

Martin G, Lenormand T, Goodnight C (2006) The fitness effect of mutations across environments: a survey in light of fitness landscape models. Evolution 60:2413–2427. doi: 10.1554/06-162.1

Martincorena I, Luscombe NM (2013) Non-random mutation: The evolution of targeted hypermutation and hypomutation. BioEssays 35:123–130. doi: 10.1002/bies.201200150

Matthews B, Aebischer T, Sullam KE, Lundsgaard-Hansen B, Seehausen O (2016) Experimental Evidence of an Eco-evolutionary Feedback during Adaptive Divergence. Curr Biol 26:483–489. doi: https://doi.org/10.1016/j.cub.2015.11.070

McAllan BM, Feay N, Bradley AJ, Geiser F (2012) The influence of reproductive hormones on the torpor patterns of the marsupial Sminthopsis macroura: Bet-hedging in an unpredictable environment. Gen Comp Endocrinol 179:265–276. doi: 10.1016/j.ygcen.2012.08.024

Merico A, Brandt G, Smith SL, Oliver M (2014) Sustaining diversity in trait-based models of phytoplankton communities. Front Ecol Evol 2:59. doi: 10.3389/fevo.2014.00059

Merow C, Dahlgren JP, Metcalf CJ, Childs DZ, Evans ME, Jongejans E, Record S, Rees M, Salguero-Gómez R, McMahon SM, Ramula S (2014) Advancing population ecology with integral projection models: a practical guide. Methods Ecol Evol 5:99–110. doi: 10.1111/2041-210X.12146

Moritz C, Agudo R (2013) The Future of Species Under Climate Change: Resilience or Decline? Science 341:504. doi: 10.1126/science.1237190

Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskel MA, Kingsolver JG, Maclean HJ, Masel J, Maughan H, Pfennig DW, Relyea RA, Seiter S, Snell-Rood E, Steiner UK, Schlichting CD (2015) Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. Heredity 115:293–301. doi: 10.1038/hdy.2015.8

Murren CJ, Maclean HJ, Diamond SE, Steiner UK, Heskel MA, Handelsman CA, Ghalambor CK, Auld JR, Callahan HS, Pfennig DW, Relyea RA, Schlichting CD, Kingsolver J (2014) Evolutionary Change in Continuous Reaction Norms. Am Nat 183:453–467. doi: 10.1086/675302

Mustin K, Dytham C, Benton TG, Travis JMJ (2013) Red noise increases extinction risk during rapid climate change. Divers Distrib 19:815–824. doi: 10.1111/ddi.12038

Nussey DH, Wilson AJ, Brommer JE (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evol Biol 20:831–844. doi: 10.1111/j.1420-9101.2007.01300.x

Odegard VH, Schatz DG (2006) Targeting of somatic hypermutation. Nat Rev Immunol 6:573.

Ohta T (1973) Slightly Deleterious Mutant Substitutions in Evolution. Nature 246:96.

Philippi T (1993) Bet-Hedging Germination of Desert Annuals: Variation Among Populations and Maternal Effects in Lepidium lasiocarpum. Am Nat 142:488–507. doi: 10.1086/285551

Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? Trends Ecol Evol 20:481–486. doi: 10.1016/j.tree.2005.06.001

Platt JR (1964) Strong Inference. Science 146:347. doi: 10.1126/science.146.3642.347

Posadas DM, Carthew RW (2014) MicroRNAs and their roles in developmental canalization. Curr Opin Genet Dev 27:1–6. doi: https://doi.org/10.1016/j.gde.2014.03.005

Reed TE, Schindler DE, Hague MJ, Patterson DA, Meir E, Waples RS, Hinch SG (2011) Time to Evolve? Potential Evolutionary Responses of Fraser River Sockeye Salmon to Climate Change and Effects on Persistence. PLOS ONE 6:e20380. doi: 10.1371/journal.pone.0020380

Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT (2010) Phenotypic plasticity and population viability: the importance of environmental predictability. Proc R Soc B Biol Sci. doi: 10.1098/rspb.2010.0771

Reusch TBH (2014) Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. Evol Appl 7:104–122. doi: 10.1111/eva.12109

Romero-Mujalli D, Cappelletto J, Herrera EA, Tárano Z (2017) The effect of social learning in a small population facing environmental change: an agent-based simulation. J Ethol 35:61–73. doi: 10.1007/s10164-016-0490-8

Romero-Mujalli D, Jeltsch F, Tiedemann R (2018) Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions. Reg Environ Change. doi: 10.1007/s10113-018-1406-7

Rudman SM, Schluter D (2016) Ecological Impacts of Reverse Speciation in Threespine Stickleback. Curr Biol 26:490–495. doi: https://doi.org/10.1016/j.cub.2016.01.004

Schlichting CD, Wund MA (2014) Phenotypic plasticity and epigenetic marking: an assessment of evidence for genetic accommodation. Evolution 68:656–672. doi: 10.1111/evo.12348

Schwager M, Johst K, Jeltsch F, Associate Editor: Wolf M. Mooij, Editor: Michael C. Whitlock (2006) Does Red Noise Increase or Decrease Extinction Risk? Single Extreme Events versus Series of Unfavorable Conditions. Am Nat 167:879–888. doi: 10.1086/503609

Shaver AC, Dombrowski PG, Sweeney JY, Treis T, Zappala RM, Sniegowski PD (2002) Fitness evolution and the rise of mutator alleles in experimental Escherichia coli populations. Genetics 162:557–566.

Shefferson RP, Salguero-Gómez R (2015) Eco-evolutionary dynamics in plants: interactive processes at overlapping time-scales and their implications. J Ecol 103:789–797. doi: 10.1111/1365-2745.12432

Stillman RA, Railsback SF, Giske J, Berger U, Grimm V (2015) Making Predictions in a Changing World: The Benefits of Individual-Based Ecology. Bioscience 65:140–150. doi: 10.1093/biosci/biu192

van Buskirk J, Mulvihill RS, Leberman RC (2009) Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. Glob Change Biol 15:760–771. doi: 10.1111/j.1365-2486.2008.01751.x

van Gestel J, Weissing FJ (2016) Regulatory mechanisms link phenotypic plasticity to evolvability. Sci Rep 6:24524.

Vasseur DA, Yodzis P (2004) The color of environmental noise. Ecology 85:1146–1152. doi: 10.1890/02-3122

Via S, Lande R (1985) Genotype-Environment Interaction and the Evolution of Phenotypic Plasticity. Evolution 39:505–522. doi: 10.2307/2408649

Vincenzi S (2014) Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. J R Soc Interface 11:20140441. doi: 10.1098/rsif.2014.0441

Visser ME, te Marvelde L, Lof ME (2012) Adaptive phenological mismatches of birds and their food in a warming world. J Ornithol 153:75–84. doi: 10.1007/s10336-011-0770-6

West-Eberhard MJ (2003) Developmental Plasticity and Evolution. Oxford University Press, New York

Wiens JJ (2016) Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. PLOS Biol 14:e2001104. doi: 10.1371/journal.pbio.2001104

Wright TF, Eberhard JR, Hobson EA, Avery ML, Russello MA (2010) Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethol Ecol Evol 22:393–404.

Yoshida T, Jones LE, Ellner SP, Fussmann GF, Hairston NG (2003) Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424:303–306. doi: 10.1038/nature01767

Danksagung

Ich werde ab und zu auf Spanisch schreiben. Damit habt Euch ein Teil meiner Wurzeln. Der andere Teil ist arabisch, aus dem Libanon. Zuerst will ich meinen Betruer Ralph Tiedemann und Florian Jeltsch bedanken. Insbesondere für die Möglichkeit, das Vertrauen, Geduld, Unterstützung und wunderbare konstruktive Kommentare und Feedbacks. Thanks very much to the team of my research school (PhDs and supervisors) at the University. Especial and BIG thanks to Sofia Paraskevopoulou, Sandra Kahl and Remco Folkertsma. It was a great experience, time, and moments with you guys: brainstorming, cookies, beers, and materialization of our joint ideas. I am looking forward to our next FSP meeting in Madrid! Many thanks to all my colleagues, from both groups! So great to have always present the movies of Star Trek with Captain Dirk leading the Enterprise, and Star Wars, when jumping from one side of the force to the other. It remains your task to guess which one was the Dark side muahahaha. Herzlichen Dank auch für die Deutschunterrichten!

Vielen Dank Hannes für die Organisation und Einladungen zu den Bierrunde, und, vor allem, für die Tipps und Gestaltungsideen für diese Dissertation. Ich habe dir gesagt! Du weißt was ich meine :P. Many thanks also to Julia for supporting me with last moment translations of the summary!

Gracias especiales a mis amistades! a Pier! Grazie mille Ragazzo! Looking forward to playing the guitar in Italy. Sissita!! Me salvaste la vida con tu apartamento! Y vaya que me ayudó a disfrutar de Potsdam y Berlín como no pude antes. Gracias por el apoyo, los chistes, risas, charlas filosóficas, bailes, música, excursiones (en bici y a pié), viajes, ... por ser y estar, por aparecer en esos momentos, y más: Merlin, Adri, Rob, Evans, Shubby, Hadi, Edu, Bel Ana, Claudia ...

Gracias inmensas a mis padres, mi hermano y mi familia toda. Seguimos adelante que sí se puede! Haciendo camino al andar. Quisiera escribir el punto y final de esta disertacion junto al numero 33 que me acompañó durante este año como si fuese inducido por las ondas gravitacionales enviadas por Cooper desde el agujero negro: Confianza y fe que lo lograrás! 33.

Eidesstattliche Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation „Ecological Modelling of Adaptive Evolutionary Responses to Rapid Climate Change“ von mir eigenständig und ohne unerlaubte Hilfe verfasst wurde und ich keine anderen als die zitierten Quellen und Hilfsmittel verwendet habe. Weiterhin erkläre ich, dass diese Arbeit noch keiner anderen Hochschule im In- oder Ausland zur Prüfung vorgelegt wurde.

Potsdam, den 21.06.2019

Daniel Romero Mujalli