

Modelling the Evolution of Species' Ranges

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Doctoral thesis



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Cover illustration: Simulation of the genic variance during 20,000 generations of range expansion with the recombination rate between neighbouring loci set to $c = 10^{-4}$ (for further details, refer to Paper I). Simulations were performed using the Matlab code available at <https://doi.org/10.5061/dryad.95x69p8h5>.

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Abstract

The fact that species have limited ranges is often due to a limited ability to adapt to the environmental conditions that occur outside their geographic ranges. However, due to ongoing climate change, the environmental conditions *within* species' geographic ranges may change in the near-future. To avoid extinction, many populations therefore need to migrate to new areas and/or adapt to the new conditions.

Migration to new areas may be problematic, however, because adaptation to new environmental factors, such as predation/grazing, competition, or parasitism from new species, or new physical factors besides temperature, may be necessary even though the temperature is the same in the new area as in the native habitat. In addition, migration to new areas is associated with a considerable loss of genetic diversity, which may severely reduce the ability to adapt to new conditions. To understand if and how populations may adapt to new environments, or if their ranges will contract when the environmental conditions change, it is necessary to understand which evolutionary mechanisms underly the geographic range limits of species.

In my dissertation, I am using mathematical and computer-based modelling to study the limits to evolution at range margins. I find, among other things, that the ability to self-fertilise often is favourable at range margins, despite the depletion of genetic diversity that is typically associated with self-fertilisation. Likewise, I find that it is often favourable for range expansions if combinations of genes that are under selection tend to be inherited together (rather than being mixed up under so-called genetic recombination), in part because locally adapted combinations of genes are partially protected from being mixed up with less well-adapted genes. It is known that another factor that facilitates range expansions is phenotypic plasticity: that is, the ability of an organism to change its characteristics (phenotype) as a response to the environment it is exposed to. I find that evolution favours increased plasticity only as long as the cost of plasticity is not too high. To interpret empirical experiments involving plasticity correctly it is important to know if the observed change in phenotype improves the local fitness or if it is just a consequence of physiological stress, which I illustrate with simulations. Finally, I find that the effects of multiple environmental gradients (gradual changes in the environmental conditions across geographical space) are added to each other in such a way that the total environmental gradient may become steep enough to prevent further range expansion, even when each individual gradient is shallow and easy to miss in field studies. To conclude, the new insights from my thesis contribute to improving the understanding of why limits to species' ranges form.

Keywords: Range expansions, range margins, population genetics, evolutionary biology, local adaptation, environmental selection, phenotypic plasticity, computer simulations.

Populärvetenskaplig sammanfattning

Att arter har begränsade geografiska utbredningsområden beror ofta på en begränsad förmåga att anpassa sig till de miljöförhållanden som råder utanför arternas utbredningsgränser. På grund av pågående klimatförändringar kan dock de miljöförhållanden som råder *inom* arters nuvarande utbredningsområden komma att ändras inom den närmaste framtiden. För att undgå utrotning kommer därför många populationer att behöva migrera till nya områden och/eller anpassa sig till de förändrade livsförhållandena.

Migration till nya områden är inte oproblemiskt eftersom anpassning till andra miljöfaktorer, såsom predation/betning, konkurrens eller parasitism från nya arter, eller nya fysiska faktorer utöver temperatur, kan krävas även om temperaturen i det nya området är densamma som temperaturen i det ursprungliga habitatet. Därtill är migration till ett nytt område ofta förknippat med en betydande förlust av genetisk diversitet inom populationer, vilket i sig kan leda till en kraftig reduktion av populationens förmåga att anpassa sig till nya förhållanden. För att förstå om och hur populationer kan anpassa sig till de nya förhållandena, eller om deras utbredningsområden kommer krympa när livsbetingelserna förändras, är det nödvändigt att förstå vilka evolutionära mekanismer som ligger bakom att arter har bestämda gränser för sina utbredningsområden.

I min avhandling använder jag matematisk och datorbaserad modellering för att studera evolutionens begränsningar i de livsmiljöer som råder vid arters utbredningsgränser, och vilka faktorer som gynnar större utbredningsområden. Jag finner, bland annat, att förmågan till självbefruktning ofta är gynnsam i marginella och glest befolkade miljöer, trots den negativa effekt som självbefruktning vanligtvis har på populationer genom att bidra till reducerad genetisk diversitet. Likaså finner jag att det ofta är gynnsamt för expansion av utbredningsområden om kombinationer av gener under selektion tenderar att nedärvas tillsammans (istället för att blandas upp under så kallad genetisk rekombination), bland annat för att lokalt anpassade kombinationer av gener delvis skyddas från att blandas ihop med sämre anpassade gener. Det är känt att ytterligare en faktor som kan gynna expansion av utbredningsområden är fenotypisk plasticitet, dvs förmågan för en organism att förändra sina egenskaper (fenotyp) som ett svar på den miljö den exponerats för. Jag finner att evolutionen bara gynnar ökad plasticitet så länge kostnaderna för plasticitet inte är för stora. För att korrekt tolka empiriska experiment involverande plasticitet är det viktigt att veta om den förändrade fenotyp som observerats bidrar till att öka den lokala anpassningsförmågan eller om den snarare är en konsekvens av fysiologisk stress, vilket jag illustrerar med simuleringar. Slutligen finner jag att multipla miljögradienter (gradvisa förändringar av livsmiljön över det geografiska rummet) adderas till varandra så att den totala gradienten kan bli tillräckligt brant för att förhindra vidare expansion av en populations utbredningsområde. Detta även om individuella gradienter är grunda och lätt kan missas i fältstudier. Sammanfattningsvis bidrar de nya insikterna från min avhandling till att öka förståelsen för varför gränser för arters utbredningsområden bildas.

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List of publications

The thesis is based on the following papers, referred to in the text by their roman numerals:

Paper I: Eriksson, M., & Rafajlović, M. (2021). The effect of the recombination rate between adaptive loci on the capacity of a population to expand its range. *The American Naturalist*, 197(5), 526-542.

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Paper II: Eriksson, M., & Rafajlović, M. (2022). The role of phenotypic plasticity in the establishment of range margins. *Philosophical Transactions of the Royal Society B*, 377(1846), 20210012.

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Paper III: Eriksson, M., Kinnby, A., De Wit, P., & Rafajlović, M. (2022). Adaptive, maladaptive, neutral, or absent plasticity: Hidden caveats of reaction norms. *Evolutionary Applications*. Accepted (in print).

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Paper IV: Tomasini, M., Eriksson, M., Johannesson, K., & Rafajlović, M. (2022). Species' ranges and the steepening-gradient hypothesis. *bioRxiv*.

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My contribution

Paper I-II: I wrote the simulation code, interpreted the simulation results, did the analytical calculations and wrote the manuscript with input from Marina Rafajlović.

Paper III: I wrote the simulation code, interpreted the simulation results, did statistical analyses, and wrote the manuscript with input from Pierre De Wit, Alexandra Kinnby and Marina Rafajlović.

Paper IV: I wrote the simulation code. I provided feedback on the interpretation of the results, on the analytical calculations, and on the manuscript text.

Introduction

The geographic distribution of species

Anyone who has travelled has probably observed that different geographic areas host different species of organisms. Some of us might have wondered why this is the case. What determines in which geographic locations a species can be found? Unfortunately, there is no simple, general answer to why each species occupies its specific geographic range (Willi & Van Buskirk 2019). Instead, there are many factors that to various degrees may be involved in shaping the geographic distribution of species. These include, but are not limited to, the past and the present climate (Hampe & Jump 2011; de Lafontaine, et al. 2018; Freeman et al. 2018; Charitonidou et al. 2021), the movement of tectonic plates (Sterrer 1973; Keith et al. 2013; Heads, 2019), species' evolutionary history (Delsuc et al. 2020; Bridle & Hoffmann 2022), species' current physiological adaptations (Deutsch et al. 2022), and biotic interactions, such as interspecific competition (Paquette & Hargreaves 2021; Freeman et al. 2022). I will not go into details regarding all possible aspects implicated in species' geographic ranges, but I note that two important factors that limit the geographic distribution of species are: 1) the fact that each species has a finite range of environmental conditions that it can tolerate, that is, a finite niche (Holt 2003), and 2) the fact that the physical environment changes in geographic space (Holden 2005). Together, these two facts imply that not all geographic locations can be suitable for all species, and therefore that most species have limited geographic ranges (Hardie & Hutchings 2010).

That is not to say that species' geographic ranges cannot change even when the environment is stable. Species can evolve adaptations to novel environments, and thereby increase the range of conditions they can tolerate (Holt 2003). Consequently, unless range expansion is prevented by other obstacles, such as a barrier to migration, evolution may allow species to expand their geographic ranges to infinity (Bridle & Vines 2007; Willi & Van Buskirk 2019). Therefore, it is somewhat surprising that species' range limits often coincide with niche limits rather than with barriers to dispersal (Hargreaves et al. 2014; Lee-Yaw et al. 2016). Given enough time, evolution should, in principle, allow for species to have unlimited niches, and hence potentially unlimited ranges. So, the question is, what prevents further evolution at range margins? Empirical studies can provide answers for specific species (e.g., Fedorka et al. 2012; Gould et al. 2014; Lyons et al. 2016; Mauro et al. 2021; Paquette & Hargreaves 2021). However, without a theoretical understanding of the mechanisms behind the limits to evolution at range margins, the results cannot be generalised beyond the specific species, system, or environment that is studied. Therefore, empirical studies need to be complemented with theory. Accordingly, the main aim of my thesis is to improve the theoretical understanding of why and when range margins of evolving species form. But before going into details regarding the theoretical study of evolution at range margins, I start with a general discussion about geographical variation in environmental conditions and how species can produce various phenotypic adaptations to these conditions.

A gradual change in abiotic environmental properties in space is referred to as an environmental gradient (Angert et al. 2020). Environmental gradients may occur on many different scales. For instance, there is a global gradient in temperature along the longitudes of

the Earth (with higher temperatures closer to the equator and colder temperatures closer to the poles). There are also environmental gradients on smaller scales. For example, along sea shores that are subject to tides there is typically a gradient in the time that individuals are submersed below the sea surface (Harley & Helmuth 2003). Due to this gradient, there is often a layered pattern of species adapted to different degrees of exposure to sea water or air. This intertidal zonation pattern is especially pronounced along rocky sea shores, although some zonation may occur also on sandy or muddy shores (Peterson 1991). Marine organisms with low tolerance to air exposure are restricted to the zone below the lowest low tide. Higher up, organisms need to tolerate both being exposed to air and sea water. In this zone, it is common to find belts of different species of, for example, barnacles, limpets, bivalves, snails, algae, cyanobacteria, and lichens that to various degrees are adapted to these conditions (Colman 1933; Javor & Castenholz 1981; Higgins et al. 2015).

Large-scale environmental gradients may, in turn, be interrupted by rocks, rivers, lakes, mountains, farmlands, cities, or other natural or human-made features. As a consequence, the habitat may contain a mix of more and less suitable environments for a species. Depending on the dispersal potential of the species and to which degree it is a generalist or a specialist, this fragmentation of the habitat may result in partly isolated populations with only minor gene exchange between them (MacArthur & Levins 1964; Holt & Keitt 2000). Thus, there may be one or several large-scale gradients across the entire geographic distribution of a species, and then local gradients within each local population (Rakocinski et al. 1992). In addition to this spatial variability, there is usually also temporal variation in environmental conditions, which may be directional (such as increasing average temperature due to ongoing climate change), periodic (e.g., night-time or seasonal cycles), and/or random (Holt et al. 2022). The combined environmental variation in time and space dictates which environments an individual will encounter during its lifetime, depending on its longevity and mobility. In turn, the experienced environments, in combination with the individual's phenotypic adaptations during its development (potentially including very different development stages, such as larval or adult stages), determine the individual's fitness, that is, the expected number of surviving offspring that the individual produces during its lifetime (Sæther & Engen 2015).

Because the phenotype of an individual determines its fitness in a given environment, the phenotype also governs which geographic locations along an environmental gradient are suitable for the individual during its different life stages. For each phenotypic trait, the trait value is in part determined by the genetics of the organism, and in part a consequence of the environmental conditions that the organism has experienced (Des Roches et al. 2018). The part of the trait value that is affected by the environment is referred to as phenotypic plasticity, or plasticity for short (Schneider 2022).

Genetic differentiation along an environmental gradient can give rise to different phenotypes that are adapted to different environments (Linhart & Grant 1996; Hereford 2009; Savolainen et al. 2013; Montejo-Kovacevich 2022), and is therefore an important component for determining the extent of a species' geographic range. A good illustration of genetic differentiation is provided by the rough periwinkle (*Littorina saxatilis*). This snail species exists in several ecotypes with distinct differences in phenotype (Johannesson et al. 2010;

Butlin et al. 2014). For example, there is one ecotype with a thick shell that can better withstand crab attacks (Figure 1). Then, there is another, much smaller ecotype that has a thinner shell and a relatively larger foot area compared to the size of the shell. These adaptations reduce the drag force from waves and allow individuals to better cling on to cliffs (Le Pennec et al. 2017). Thus, the large ecotype is favoured in areas where predatory crabs are abundant, whereas the small ecotype is favoured in wave-exposed areas. Interestingly, these two ecotypes appear to have evolved in parallel throughout the species' range. That is, individuals from the same geographic location are more genetically similar to each other, independent of ecotype, than individuals of the same ecotype but from different geographic locations (Butlin et al. 2014). Chromosomal inversions, which are genomic regions of low recombination, play an important role in maintaining local adaptation for this species, and possibly also in facilitating repeated parallel evolution (Faria et al. 2019; Koch et al. 2021; Westram et al. 2022).



*Figure 1: The crab ecotype of *Littorina saxatilis*. This ecotype has a thick shell that provides protection from predatory crabs, making it locally adapted to environments where crabs are abundant, whereas the smaller wave ecotype is locally adapted to wave-swept environments. The picture shows the crab ecotype from Sweden. A similar division into two ecotypes also occurs in Spain and in the UK (Johannesson et al. 2010; Butlin et al. 2014). Photo credit: Daria Shipilina.*

In addition to genetic differentiation, phenotypic diversity can be generated by phenotypic plasticity. That is, from the same genotype, different phenotypes may be formed as a response to the environmental conditions (Bradshaw 1965; Pfennig 2021), making plasticity a potentially faster way than evolution for populations to adapt to new conditions. Plasticity may itself be genetically encoded, and therefore able to evolve (Pfennig 2021). Because it allows for different phenotypes to be produced without any requirement for genetic variation, plasticity may be a fruitful strategy for populations to expand their geographic ranges or to adapt rapidly to a changing environment (West-Eberhard 2005; Nicotra et al. 2010; Levis & Pfennig 2016; Johannsson et al. 2017; Corl et al. 2018; Perry et al. 2018).

However, plasticity is a more complex concept than it might appear to be upon a first glance, and there are many possible ways for individuals to express plasticity (Schneider 2022). For

example, plasticity may be adaptive, so that the phenotype that is created by the plastic response grants an individual a higher fitness than the fitness for the phenotype without the plastic response. However, plasticity may also be maladaptive and decrease the fitness of the individual (Schneider 2022). Furthermore, plasticity may be either an active response to the environmental conditions that the individual is exposed to, or a passive consequence of the environmental conditions. Passive plasticity in fitness-indicator traits (i.e., traits having a trait value that is correlated to fitness) is often a sign of stress or resource limitation rather than an adaptive response, as the trait values of these traits are preferably kept constant in stressful environments (Reusch 2014; Bonser 2021). If plasticity is an active response, it relies on environmental cues that inform the organism which environmental conditions are likely to occur in the future. The environmental cues may be more or less reliable, and their reliability depends in part on how long the plastic response is delayed after the observation of the cues, how variable the environment is, and how predictable the variability of the environment is. If environmental cues are unreliable, the utility of plasticity is limited because high plasticity would potentially lead to ‘overfitting’ to the environment, and as a consequence, plasticity would be potentially maladaptive. Under such unpredictably fluctuating environmental conditions, a less plastic phenotype is usually preferable (Bitter et al. 2021). Another possible limitation to plasticity is that there may be a fitness cost associated with the ability to be plastic. There could, for example, be a metabolic cost for maintaining the sensory and regulatory systems necessary for perceiving environmental cues and responding by plasticity (Murren et al. 2015; Schneider 2022). Such costs would imply a trade-off between the benefit of plasticity and its costs. Furthermore, the plastic responses may be reversible or irreversible, which also affects whether plasticity is likely to be adaptive or not (Schneider 2022). Thus, it is currently unclear how plasticity affects adaptation at range margins.

The plastic and non-plastic components of a trait may attain either continuous or discrete trait values (Orr 2005; Schneider 2022). If the trait values are continuous, the plastic and non-plastic components of the trait value can be illustrated using reaction norms (Chevin et al. 2010; Figure 2). The intercept of the reaction norm is the non-plastic component and the slope of the reaction norm is the plastic component of the trait value. Reaction norms parallel to the x -axis imply that the population does not have any plasticity in the assessed trait. Empirically, reaction norms may be obtained, for example, in a reciprocal transplant experiment, which is a typical way to infer whether there is local adaptation, plasticity, and/or interactions between the environment and the genotype (gene-environment interactions) between two different populations (Svensson et al. 2018; Johnson et al. 2022).

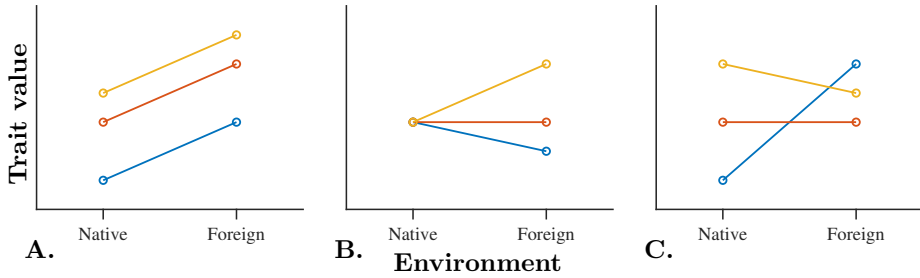


Figure 2: Phenotypic differences among environments can be represented using reaction norms. Non-zero slopes of the reaction norms indicate plasticity. Variation in intercept means that the population has standing genetic variation in the non-plastic component of adaptation, whereas variation in slopes means that the population has standing genetic variation in plasticity. Standing genetic variation in plasticity is usually referred to as gene-environment interaction (Kelly 2019). When there is sufficient standing genetic variation in either of the two kinds of traits, the traits have the potential to evolve relatively rapidly when the environmental conditions change (Blows & McGuigan 2015). Otherwise, evolution is likely to be slow because locally beneficial de novo mutations need to occur. Three qualitatively different patterns are shown in the figure: genetic variance in the non-plastic component of the phenotype, but no genetic variance in plasticity (A), genetic variance in plasticity, but not in the non-plastic component (B), and genetic variance in both the plastic and non-plastic component (C). The rings denote the phenotypic values in native and foreign environments and different colours denote different genotypes.

In sum, the range of phenotypes that can be generated, and consequently the potential geographic range of a population, is determined in part by genetic differentiation and in part by phenotypic plasticity. However, as stated in the beginning of the introduction, evolution can in the long run create new genetic adaptations or increase the plasticity of a population (Bridle & Vines 2007; Chevin et al. 2010; Bridle & Hoffmann 2022). Thereby, the range of possible environments that the population can tolerate may increase through evolution, unless there is a limit to evolution at the range margins. To fully understand the long-term fate of species ranges, it is therefore necessary to study evolution at range margins. This topic will be discussed in detail next.

Limits to evolution at the edge of a species' range

Recall that geographic ranges are often determined by habitat suitability, rather than being set by dispersal barriers (Hargreaves et al. 2014; Lee-Yaw et al. 2016), which suggests that lack of local adaptation often limits the distribution of species. This implies that there must somehow be a limit to the evolution at range margins if the geographic distribution of the species is in equilibrium¹. I will discuss geographic distributions that are not in equilibrium in the next section. In this section, I focus my attention on the limits to evolution at equilibrium range margins.

¹ More precisely, quasi-equilibrium, because the true equilibrium for any species is global extinction (Eriksson et al. 2013). However, to keep the text simple, I will avoid this technicality from now on and always refer to quasi-equilibrium range margins as equilibrium range margins.

Many possible mechanisms have been suggested that may limit the evolution at range margins, either by themselves or in combination (for reviews see, for example, Hoffmann & Blows 1994; Willi & Van Buskirk 2019; Angert et al. 2020; Bridle & Hoffmann 2022). One suggested explanation to why there are limits to evolution at range margins is given by the swamping hypothesis (Haldane 1956; Lenormand 2002). According to this hypothesis, locally adapted genotypes are prevented from being established in range margins because gene flow from core populations (typically assumed to have higher population densities than marginal populations) is so high relative to the population size of the marginal populations that it swamps local adaptation in the range margins. In an influential theoretical paper by Kirkpatrick and Barton (1997), it was shown that under the assumption of stabilising selection towards an optimal phenotype that changes linearly in space, and for a population with constant genetic variance, swamping may indeed limit adaptation at range margins. Using a deterministic diffusion approximation for gene flow in a one-dimensional habitat, it was shown that, for a given value of the genetic variance, there is a critical environmental gradient, b_c , in the optimal phenotype. When the environmental gradient is larger than b_c , gene flow prevents the population from being perfectly adapted to the entire habitat. Consequently, the gradient in the average population phenotype is too shallow to track the environmental optimum (Figure 3 A). This causes populations far from the centre of the habitat to be locally maladapted and hence small (Figure 3 B). Because these populations are small due to maladaptation, gene flow from the central part of the range further reduces the fitness in the edges, causing positive feedback between maladaptation and small population size. Thus, the population remains well adapted only in the centre of the habitat (Kirkpatrick & Barton 1997). Case & Taper (2000) later showed that the presence of a competing species can make the critical gradient considerably shallower, although competition alone (in the absence of an environmental gradient) would not restrict the range of populations at evolutionary equilibrium.

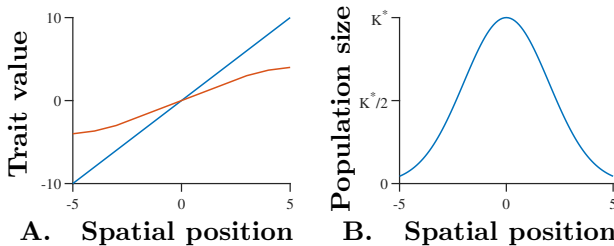


Figure 3: For a given fixed value of the genetic variance, there is a maximal environmental gradient that a population can adapt to. When the environmental gradient (panel A, blue line) is steeper than this critical gradient, the steepness of the gradient in the average phenotype of the population (panel A, red line) is shallower than the gradient in optimal phenotype because maladaptive gene flow from neighbouring populations prevents local adaptation. This causes maladaptation, and hence a small local population size, of the populations in the edges. Due to the small population size in the edges (panel B), asymmetric gene flow from the centre to the edges further reduces local fitness in the edges and prevents locally well-adapted phenotypes from evolving (see also Figure 1 in Bridle & Vines, 2007). The population size in panel B is given in terms of the re-scaled local carrying capacity (accounting for the fitness reduction due to genetic variance; Kirkpatrick & Barton, 1997), i.e., $K^* = K(1 - V_P/2r_mV_S)$, where K is the carrying capacity, V_P is the phenotypic variance, r_m is the maximal intrinsic growth rate, and V_S is the width of stabilising selection.

However, the currently available empirical evidence does not support the swamping hypothesis as a general explanation for the formation of range margins. First, although population densities may be higher in the centre of species' geographical distributions than in the edges, this is not a general rule (Sagarin & Gaines 2002; Pironon et al. 2017; Santini et al. 2019). Second, there is little empirical evidence that gene flow in general has negative fitness effects on range margins (Kottler et al. 2021). In accordance with the empirical data, several theoretical studies on the evolution of species' ranges published after Kirkpatrick & Barton (1997) and Case & Taper (2000) suggest that the net effect of gene flow is often positive rather than negative (e.g., Barton 2001; Polechová & Barton 2015; Polechová 2018; Polechová 2022). Indeed, Barton (2001) showed that when the genetic variance is allowed to evolve (ignoring linkage disequilibria and assuming either two possible alleles or a normally distributed continuum of allelic effect sizes at each locus), gene flow does not limit adaptation at range margins. On the contrary, gene flow allows the evolution of sufficient genetic variance to make it possible for the population to expand its range indefinitely and reach perfect adaptation throughout the entire habitat. Infinite range expansion is prevented only when the genetic load due to the variance that evolves becomes so high that it causes the mean growth rate to drop below zero. As an illustrative example for when the genetic load can be this high, consider a population with a logistic population growth model. That is, assume that the individual growth rate in an environment where the optimal phenotypic value is θ , the population size is N , and the carrying capacity is K , is

$$r(z, N) = r_m \left(1 - \frac{N}{K}\right) - \frac{(z-\theta)^2}{2V_S}, \quad (1)$$

for an individual with phenotypic value z . Here, r_m is the maximal intrinsic growth rate and V_S is the width of stabilising selection. Then, the population growth rate is

$$\bar{r}(\bar{z}, N) = r_m \left(1 - \frac{N}{K}\right) - \frac{(\bar{z}-\theta)^2}{2V_S} - \frac{V_P}{2V_S}. \quad (2)$$

Here, V_P denotes the phenotypic variance. By setting $\bar{z} = \theta$ and $N = 0$ (i.e., by maximising the population growth rate) it follows that the mean population growth rate is negative when

$$r^* = r_m - \frac{V_P}{2V_S} < 0. \quad (3)$$

For genetic variance V_G , environmental variance V_E , steepness of the environmental gradient b , and standard deviation of the dispersal distance σ (assuming Gaussian dispersal), and under the assumption of either bi-allelic loci or a normally distributed continuum of allelic effect sizes at each locus, it can be shown that the phenotypic variance is, in turn, given by $V_P = V_G + V_E = b\sigma\sqrt{V_S} + V_E$ (Barton 2001). In order for this hypothetical population to have a finite but non-zero equilibrium range it is necessary that the inequality in equation (3) is satisfied in the edges of the habitat, but not in the centre. This means that either the steepness of the environmental gradient (b), the standard deviation of the dispersal distance (σ), the intensity of stabilising selection ($1/V_S$), the environmental variance (V_E), or a combination of these parameters, need to increase in space (or the maximal intrinsic growth rate, r_m , needs to decrease) for a population to have a finite equilibrium range. This example suggests another explanation for why range margins may form. Even if dispersal, in contrast to the model by

Kirkpatrick & Barton (1997), does not move the average phenotype of marginal populations away from the local optimum (compare to Figure 3A; in the model by Barton (2001) the red and the blue lines would coincide), dispersal may still reduce the local mean fitness by inflating the genetic variance. Consequently, stable range margins may form where the genetic load caused by dispersal locally becomes so high that the population cannot maintain a positive growth rate. I will hereafter refer to this hypothesis for the formation of range margins as the *steepening-gradient hypothesis* because it implies that range margins may occur where the environmental gradient is steepening.

The model by Barton (2001) was deterministic and therefore it did not account for the stochastic effects that are likely to be strong if the populations in the range margins are small (Crow & Kimura 1970; see also Bridle et al. 2010). In Polechová & Barton (2015), the model by Barton (2001) was accordingly refined by the inclusion of stochastic effects on population dynamics. It was thus shown that local adaptation fails in a one-dimensional habitat, leading to stable range margins, when the fitness cost of dispersal is sufficiently high compared to the efficacy of selection relative to drift², that is when

$$B \gtrsim 0.15N\sigma\sqrt{s}. \quad (4)$$

Here, $1/(N\sigma)$ is the strength of drift (i.e., the reciprocal of the population size within a dispersal distance) for a haploid population, $s = \alpha^2/2V_S$ (where α is the allelic effect size) is the strength of selection per locus, and B indicates the effective environmental gradient, defined as

$$B = \frac{b\sigma}{r^*\sqrt{2V_S}}. \quad (5)$$

The effective environmental gradient B takes into account all biotic and abiotic factors that influence the fitness effect of a trait under environmental selection. Equation (4) implies that range margins form in locations where the joint effects of drift and genetic load due to gene flow are too strong in comparison to selection. There are a few ways in which the condition in equation (4) can be satisfied. Local adaptation fails, and stable range margins form, when:

- 1) The local steepness of the effective environmental gradient is too high. That is, when the fitness cost incurred by dispersal to neighbouring habitat patches is too high.
- 2) The local carrying capacity is too low. This may be because the quality of the local habitat patches is too low or because the competition for resources is too high.
- 3) The dispersal between neighbouring local populations is either too high (causing too high genetic load) or too low (making the neighbourhood size too small and therefore drift too strong).

Note that dispersal has two counteracting effects. On the one hand, dispersal reduces the mean fitness by increasing the genetic variance. On the other hand, dispersal may reduce drift caused by local isolation. Consequently, intermediate dispersal is optimal for the geographic

² Strictly speaking, four parameters are needed to completely describe the system. However, two of them – the strength of selection relative to the strength of density dependence (s/r^*) and the mutation rate relative to the strength of density dependence (μ/r^*) – are usually very small and may be neglected.

distribution of a population, meaning that dispersal can be both positive and negative for marginal populations depending on the circumstances. Note that with smoothly changing parameters, adaptation may fail abruptly, leading to a sharp range margin (see, for example, Figure 3 in Polechová & Barton 2015). This is in contrast to the deterministic model by Barton (2001) where smoothly changing parameters imply that the population size decreases smoothly to zero. The results from Polechová & Barton (2015) are thus consistent with the lack of empirical support for the abundant centre hypothesis as a general biogeographic rule (Santini et al. 2019). The reduction in local population density close to the range margin, relative to the population density in the centre, may be so small that it is hard to detect empirically.

In Polechová (2018) the model in Polechová & Barton (2015) was extended to a two-dimensional habitat (but with a gradient only in one dimension). Interestingly, it was found that the prediction for where local adaptation fails has a simpler form in two-dimensional habitats than in one-dimensional habitats: the main parameters that determine where range margins form in two-dimensional habitats are the fitness cost of dispersal and the strength of drift (whereas the fitness cost of dispersal and the efficacy of selection relative to drift are the main parameters in one-dimensional habitats; i.e., the dependency on selection vanishes in two dimensions). More precisely, in two dimensions, adaptation fails when (here $\pi \approx 3.1416$ denotes the ratio of a circle's circumference to its diameter, the other parameters are as defined above)

$$6.3B + 0.56 \gtrsim 2\pi N\sigma^2. \quad (6)$$

Note that in two-dimensional habitats, the neighbourhood size increases quadratically with dispersal whereas the effective environmental gradient (equation (5)) increases approximately linearly with dispersal. Consequently, dispersal in two dimensions has a predominantly positive effect on local adaptation for marginal populations. This is true for a wide range of dispersal models, including models where long-range dispersal is possible (Polechová, 2022). Dispersal may be deleterious to local adaptation in two-dimensional habitats only when long-range dispersal is very common (i.e., for strongly leptokurtic dispersal kernels) and the environmental gradient is steep (Polechová, 2022). This result is qualitatively different from the role of dispersal in one-dimensional habitats, where both the effective environmental gradient and the neighbourhood size increases (approximately) linearly with dispersal (cf. equation (4)), so that the effects of dispersal nearly cancel out (although a weak dependence on dispersal remains through the parameter r^* , which affects both B and the equilibrium population density, making intermediate values of dispersal optimal in one-dimensional habitats; Polechová & Barton 2015).

Bridle et al. (2019) investigated range expansion in a habitat where a trait optimum that changes linearly in space is interrupted by a segment with a spatially constant trait optimum. In this case, the population in the region with a spatially constant trait optimum evolves to a state with locally low genetic variance and high density. Therefore, strongly asymmetrical gene flow from the flat region of the gradient causes high genetic load at the range edges, which prevents further range expansion. Notably, the study by Bridle et al. (2019) demonstrates that the overall shape of the environmental gradient can be important for the formation of stable range margins. A spatially non-uniform steepness of the environmental gradient can lead to asymmetric gene

flow because the realised population density along such a gradient may vary in space. Thus, equations (4) and (6) do not give the whole picture because they only account for the local conditions. However, with a smoothly steepening environmental gradient (and, consequently, a smoothly decreasing population size towards the edges of the habitat due to increasing genetic load), both Polechová & Barton (2015) and Bridle et al. (2019) found that range expansion was halted approximately at the critical gradient predicted by equation (4). This finding suggests that, unless the steepness of the environmental gradient changes very abruptly, the shape of the environmental gradient, and asymmetric gene flow, often plays a minor role in the establishment of range margins.

Recently, it has been further shown that an increasing magnitude of temporal fluctuations in environmental conditions may also lead to stable range margins (Benning et al. 2022). This is because, similarly to how genetic load due to migration can become too high when the spatial gradient in the optimal phenotype is too steep, the genetic load can be too high when the magnitude of temporal fluctuations is too large (Benning et al. 2022).

Range expansions and their impact on genetic diversity

The theoretical studies presented in the previous subsection predict when equilibrium range margins are expected to form. However, environmental conditions do not necessarily remain stable for the time needed to reach equilibrium, especially when interactions with other populations are considered (Alexander et al. 2022). Range margins may, thus, better be considered as dynamical rather than stable (Holt 2003). For a complete picture of range margins, we therefore also need to consider ongoing range expansions and their effects on genetic diversity. This is particularly important in the present day, because ongoing global climate change causes rapidly changing environmental conditions (e.g., Makino et al. 2014; Jonsson et al. 2018; Charitonidou et al. 2021).

Recall that in order for a population to expand its range, it is necessary that it has the genetic variance needed for continued range expansion (Kirkpatrick & Barton 1997; Hardie & Hutchings 2010; Angert et al. 2020). However, range expansions are themselves associated with a loss of genetic diversity (Robalo et al. 2012, Rózsa et al. 2016). This can be illustrated by considering genetic drift in a population (Crow & Kimura 1970). When self-fertilisation is allowed in a randomly mating population inbreeding reduces the population heterozygosity. For a population with a constant population size of $N = K$ individuals and a starting heterozygosity of H_0 , the heterozygosity is by the n^{th} generation reduced to

$$H_n = H_0 \left(1 - \frac{1}{2N}\right)^n. \quad (7)$$

When self-fertilisation is prevented, inbreeding is reduced, and the heterozygosity is in each generation reduced by (Crow & Kimura 1970)³

³ When there are two separate sexes, the population size in equation (8) should be replaced with the effective population size (Crow & Kimura, 1970)

$$H_n = H_0 \left(\frac{N-1+\sqrt{N^2+1}}{2N} \right)^n. \quad (8)$$

Note that equation (8) asymptotically approaches equation (7) as N increases. Analogously to genetic drift in time, the genetic diversity is reduced each time a new habitat patch is colonised as a population expands its range in space. Under the simplifying assumptions that a new patch is colonised by k founding individuals in every generation and that the local population immediately grows to infinite size after colonisation, the decrease in heterozygosity is (Slatkin & Excoffier 2012)⁴

$$H_n = H_0 \left(1 - \frac{1}{2k} \right)^n. \quad (9)$$

Because the number of founders is usually small (i.e., $k \ll K$), the repeated population bottlenecks, called founder effects, that are experienced by an expanding population, may be severe. Serial founder effects may, thus, result in very strong genetic drift during range expansions.

Eventually, the adaptive genetic diversity of the population may be extremely reduced due to the serial founder effects (Ramstad et al. 2013). Notably, a consequence of serial founder effects is that certain alleles can reach fixation by chance, even when they are deleterious. This phenomenon is known as gene surfing (Hallatschek & Nelson 2008; Paulose & Hallatschek 2020; Gilbert et al. 2022). Gene surfing may contribute to reducing the average fitness of the population at the expansion front. This reduction in fitness due to range expansion is known as expansion load (e.g., Peischl et al. 2013, 2015; Gilbert et al. 2017, 2018).

Spatial sorting, that is, evolution of increased dispersal ability during range expansions, can be considered as a spatial analogue of selection, just as serial founder effects can be considered a spatial analogue of genetic drift (Shine et al. 2011; Phillips & Perkins 2019; Peischl & Gilbert 2020). Spatial sorting may reduce or eliminate expansion load incurred during range expansions (Peischl & Gilbert 2020). However, unless the expanding population is rescued from expansion load by spatial sorting, expansion load, together with a lack of genetic

$$N_e = \frac{4N_f N_m}{N_f + N_m}.$$

Here, N_f and N_m are the number of females and the number of males, respectively.

⁴ A more realistic model is obtained by assuming that the maximal population size in each patch is finite (consisting of K individuals in all patches and all generations), that founder events do not occur in every generation, so that there are T generations between each founder event, and that migration between occupied patches occurs in each generation with probability m . In this case, the number of founders (k) in equation (9) should be replaced with an effective number of founders. That is k should be replaced with (Slatkin & Excoffier 2012)

$$k_e = \frac{1}{a^T/k + (1-a^T)/(K(1-a))}.$$

Here $a = 1 - 2m - 1/2K$. Note that k_e may be both larger and smaller than k depending on the other parameters (Slatkin & Excoffier 2012).

variation, can eventually cause range expansion to stop (Willi et al. 2018; Perrier et al. 2020). Unless the conditions in equation (4) or (6) are satisfied, range expansion may continue when the local genetic diversity has been replenished by migration. However, this may take thousands of generations (Peischl et al. 2013, 2015). During this time, the environment and the optimal phenotype may have changed. Thus, to understand species' contemporary range margins, it is necessary to consider not only evolutionary equilibria assuming fixed environmental conditions, but also the dynamics between evolution and the rate of change in physical geography. This may be particularly important for organisms with long generation times, or when the environment changes rapidly, as is the case today due to climate change and other human-induced stressors on biological communities (Fréjaville et al. 2021).

Thesis aims

Much progress has been made in advancing the theoretical understanding of how evolution is limited at the edge of species' ranges in recent years (Angert et al. 2020; Bridle & Hoffmann 2022). However, there are several open questions related to range margins that have been largely unexplored. My thesis sets out to answer five of these questions, which I list in the following.

What is the role of recombination in range margins?

The results from Polechová & Barton (2015) are derived under the assumption of linkage equilibrium between the adaptive loci. This is a reasonable assumption at quasi-linkage equilibrium, when selection is weak and the recombination rate is not too low relative to selection (Kimura 1965). This is because, at quasi-linkage equilibrium, the positive linkage disequilibrium (LD) that is generated by dispersal is to a first-order approximation cancelled by the negative LD that is generated by stabilising selection (Felsenstein 1977; Polechová & Barton 2015). However, this may not be a valid approximation when the recombination rate between the adaptive loci is too low, making it unclear how the formation of range margins is affected by low recombination rates between the adaptive loci.

Notably, the role of recombination during range expansions is theoretically ambiguous. On the one hand, recombination is an important means for populations to combine beneficial alleles (Fisher 1930; Muller 1932; Hill & Robertson 1966; Roze & Barton 2006) while eliminating deleterious alleles (Muller 1964; Felsenstein 1974). As a consequence, the genetic load that typically accumulates during range expansion may be much higher when the recombination rate is low than when recombination is free (Peischl et al. 2015). On the other hand, however, a low recombination rate between adaptive loci may have several advantages for local adaptation to range margins or during range expansions. First, a low recombination rate may enhance the ability of a population to adapt to new environments by preserving more genetic variance compared to when recombination is free (Felsenstein 1974). Furthermore, when the recombination rate between adaptive loci is low, beneficial combinations of alleles may be inherited as 'adaptive cassettes' that might confer a selective advantage and facilitate range expansion (Kirkpatrick & Barrett 2015; Peischl et al. 2015). Because recombination may break up locally beneficial associations between alleles, such blocks of locally adapted alleles are also partially protected from maladaptive gene flow (Mérot et al. 2020), which potentially allows the population to maintain a wider range than if recombination between the adaptive loci is free.

Elucidating the role of recombination during range expansions and in the formation of range margins is important because genomic regions with low recombination rates often play a substantial role in local adaptation (e.g., Lowry & Willis 2010; Jones et al. 2012; Fishman et al., 2013; Westram et al. 2018; Faria et al. 2019; Kess et al. 2019; Le Moan et al. 2019, 2021; Berdan et al. 2022; Matschiner et al. 2022). The question, which is explored in **Paper I** is, thus: do marginal populations benefit from a low recombination rate because locally beneficial combinations of alleles act as 'super-genes' that are protected from genetic swamping, or do

marginal populations benefit from a high recombination rate because locally deleterious alleles are more efficiently purged? Which of these two effects dominate and under what conditions?

How does the ability to self-fertilise affects the formation of range margins?

The allowance of self-fertilisation (selfing) in hermaphrodite organisms may increase inbreeding depression (Gascoigne et al. 2009), especially for small and isolated populations (compare equations (7) and (8) for small N). Because marginal populations are often small and isolated, one may thus expect a substantially increased inbreeding depression at range margins if selfing is allowed there. However, the increased homozygosity that is caused by serial founder effects during range expansion may reduce the difference in mean fitness between inbred and outbred individuals (Pujol et al. 2009; Encinas-Viso et al. 2020). As a consequence, the effect of selfing on the fitness in marginal population may not be as deleterious as one may expect based on the local population density.

In addition, when the population densities are low, which is often the case in range margins, the difficulty of finding a mate may lead to a reduced population fitness (Gascoigne et al. 2009; Kuparinen 2018). In this case, selfing may provide reproductive assurance and thereby increase the population fitness for sparse populations (Gascoigne et al. 2009; Busch & Delph 2012). In particular, selfing may allow for a single individual to colonise a new habitat (Baker 1955; Pannell & Barrett 1998), which could considerably increase the likelihood that a new habitat is colonised as well as increase the metapopulation re-colonisation rate (Pannell & Barrett 1998).

Thus, the allowance of selfing may be beneficial during range expansions and at range margins. In fact, there is empirical evidence suggesting that plants often self-fertilise in range margins (e.g., Griffin & Willi 2014; Hargreaves & Eckert 2014), even for species that under normal conditions do not predominantly self-fertilise. However, it is not clear exactly how much selfing would quantitatively change the potential of species to adapt along an environmental gradient. This topic is studied to an extent in **Paper I**, along with the role of recombination during range expansions.

How does the ability to evolve plasticity influence the formation of range margins?

That evolution of increased phenotypic plasticity may be associated with range expansions has been shown both in empirical (e.g., Johansson et al. 2017; Corl et al. 2018) and theoretical (e.g., Chevin & Lande 2011, Schmid et al. 2019) studies. Indeed, when there are no limits to plasticity, it is theoretically possible that ‘perfect’ plasticity may evolve, so that the trait value of every individual in the population is perfectly adjusted to fit the local optimum in any geographic location (Chevin & Lande 2011; Lande 2014). Thus, the evolution of plasticity may in principle allow individuals to adapt to any environment and expand indefinitely. In practice, however, plasticity is usually limited in one way or another, for instance there may be a physiological limit to the trait values that can be produced (Chevin et al. 2010). Thus, some non-plastic adaptation may be necessary for a population to expand its range, even when the adaptive trait can evolve increased adaptive plasticity. If non-plastic adaptation is necessary, the role of plasticity is unclear because evolution of increased plasticity may slow down the

evolution of the non-plastic component of the phenotype (Ghalambor et al. 2007; Fox et al. 2019).

Furthermore, when plasticity is costly, the contribution of plasticity to local adaptation may in the long run be entirely replaced by non-plastic genetic adaptation through genetic assimilation (Waddington 1953; Ehrenreich & Pfennig 2016). If this occurs throughout the range, plasticity should not increase the equilibrium range of a population compared to the equilibrium range of a non-plastic population, although plasticity could still potentially make range expansion faster (West-Eberhard 2003; Lande 2009; Levis & Pfennig 2016; Kelly 2019). However, at range margins, populations are likely to be maladapted (otherwise they could have expanded their ranges further). Because of this, marginal populations experience continued directional selection that may promote evolution of permanently elevated plasticity (Chevin & Lande 2011). Does this mean that the ability to evolve plasticity may increase the extent of the geographical distribution compared to the prediction by equation (4) even when plasticity is costly? If it does, by how much? While the evolution of plasticity in range margins or during range expansions has been studied in many previous papers (e.g., Tufto 2000, 2015; Lande 2009; Chevin & Lande 2011; King & Hadfield 2019, Leimar et al. 2019, Schmid et al. 2019), the impact of plasticity on the establishment of stable range margins along environmental gradients has not, to my knowledge, been investigated before. Thus, the aim of **Paper II** is to quantify how much the equilibrium range of a population is changed when costly plasticity may evolve.

Is plasticity adaptive or not? On the correct interpretation of reaction norms

The degree of plasticity may vary within populations (Kelly 2019). In particular the degree of plasticity may vary geographically between local populations (e.g., Münzbergová et al. 2017; Rugiu et al. 2018). The plasticity in different local populations can be estimated empirically, for example by using reciprocal transplant experiments (Svensson et al. 2018; Johnson et al. 2022). However, it is not trivial to infer from reaction norms whether plasticity is adaptive or non-adaptive. Plasticity in fitness-indicator traits is usually not adaptive. This has occasionally led researchers to make incorrect conclusions because plasticity in fitness-indicator traits incorrectly has been interpreted as adaptive plasticity (Bonser 2021). This issue is investigated in **Paper III** using a combination of simulated and empirical data.

Range expansion along multiple gradients

As explained in the introduction, there are typically multiple environmental variables that are spatially varying throughout a population's habitat. Therefore, multiple traits may need to evolve simultaneously as a population expands its range, or when the local environmental conditions change. For instance, due to climate change, populations need to adapt to changes not only in temperature, but also, for example, in precipitation (Münzbergová et al. 2017), salinity (Rugiu et al. 2018, 2021; Milec et al. 2022), or pH (Hoegh-Guldberg et al. 2007; Rheuban et al. 2018).

However, in the model by Polechová & Barton (2015), as well as in the other theoretical models cited in the introduction, it is assumed that a single trait is under selection. Even though the trait under selection may be composite, there are no obviously unambiguous ways to account

for the joint effects of multiple traits in terms of a single composite trait. For example, the effects of two traits may add up so that a high trait value of one trait compensates for a low trait value in another trait, or the optimum of each trait may be independent of what trait value the other trait has. In terms of Fisher's geometric model (Fisher 1930; Orr 2005), the angles between the traits may differ. Thus, there may be more than one way to translate the effect of multiple traits into a single trait depending on the angle between the traits. In **Paper IV**, it is investigated how range expansion is affected when selection is acting on multiple orthogonal traits relative to when the traits are parallel.

The remainder of this thesis is organised as follows. The methods I used are detailed in 'Methods'. The main results obtained in **Papers I-IV** are discussed in 'Main results and discussion'. I discuss potential avenues for future research in 'Reflections and outlook'. The papers can be found at the end of the thesis.

Methods

The overall aim of the papers in my thesis is to elucidate the general principles behind the formation of range margins for arbitrary populations, rather than investigating the geographic distribution of specific species. Accordingly, the theoretical models are general, and no particular species or habitat is considered in the models in this thesis. The main method that is used is spatially explicit individual-based (also called agent-based) simulations (DeAngelis & Mooij 2005; Epperson et al. 2010; Romero-Mujalli et al. 2019). In the following, I briefly describe the models used in the thesis and motivate their design. Details regarding the models can be found in the specific papers.

Spatial structure of the habitat

The habitat is modelled as a one-dimensional chain of demes arranged side by side so that there is a spatial ordering of the demes. Examples of approximately one-dimensional habitats in nature are streams, shores, and road verges (the latter can be a surprisingly species-rich refuge for species in an otherwise inhospitable environment; see, e.g., Gardiner et al. 2018; Phillips et al. 2020; New et al. 2021)). The isopod *Idotea balthica*, which is considered in **Paper III** lives along sea shores where it feeds on brown algae. Dispersal is modelled according to a discretised Gaussian function, so that migration is more likely between demes that are close to each other than between more distant demes. The probability to migrate from deme i to deme j is:

$$M(j, i) = \frac{1}{\sqrt{2\pi\sigma^2}} \int_{j-i-1/2}^{j-i+1/2} \exp\left(-\frac{t^2}{2\sigma^2}\right) dt. \quad (10)$$

Note that the variance of the discretized Gaussian distribution, $\sigma_d^2 = \sum (j-i)^2 M(j, i)$, is not exactly the same as the variance of the continuous Gaussian distribution (i.e., σ^2 in equation (10)), which is a caveat that needs to be kept in mind when comparing simulation results with theoretical predictions that assumes continuous Gaussian dispersal.

Fitness and selection

Because of the reliance of my work on the continuous diffusion approximation that equation (4) is based on (Polechová & Barton 2015), it is appropriate that I briefly describe fitness and selection for this model, before explaining how fitness and selection is modelled in the simulations used in my papers. In the continuous model with a single adaptive trait (a model with two adaptive traits is discussed in **Paper IV**), the growth rate of each individual has an ecological component assuming logistic growth

$$r_e(N) = r_m \left(1 - \frac{N}{K}\right), \quad (11)$$

where r_m is the maximal intrinsic growth rate and K is the carrying capacity, and a local adaptation component

$$r_g(z) = -\frac{(z-\theta)^2}{2V_S}. \quad (12)$$

In equation (12), θ is the optimal trait value and V_S is the width of stabilising selection. Thus, the growth rate for an individual with trait value z in a habitat where the local population size is N is given by

$$r(z, N) = r_m \left(1 - \frac{N}{K}\right) - \frac{(z-\theta)^2}{2V_S}. \quad (13)$$

The changes in allele frequencies and the population size are given by equations (1)-(3) in Polechová & Barton (2015). The mean Malthusian growth rate \bar{r} in equation (3) in Polechová & Barton (2015) is given by

$$\bar{r}(\bar{z}, N) = r_m \left(1 - \frac{N}{K}\right) - \frac{(\bar{z}-\theta)^2}{2V_S} - \frac{V_P}{2V_S}. \quad (14)$$

Here V_P is the phenotypic variance. By writing the phenotypic variance as the sum of the genetic and environmental sources of variation, $V_P = V_G + V_E$, the average growth rate of the population can be written as

$$\bar{r}(\bar{z}, N) = r_m \left(1 - \frac{N}{K}\right) - \frac{(\bar{z}-\theta)^2}{2V_S} - \frac{V_G}{2V_S} - \frac{V_E}{2V_S}. \quad (15)$$

However, assuming that V_E is constant in time, it can be removed by rescaling r_m and K according to

$$r_e = r_m - \frac{V_E}{2V_S}, \quad (16)$$

and

$$K_e = K \left(1 - \frac{V_E}{2r_m V_S}\right). \quad (17)$$

This makes equation (15) equivalent to

$$\bar{r}(\bar{z}, N) = r_e \left(1 - \frac{N}{K_e}\right) - \frac{(\bar{z}-\theta)^2}{2V_S} - \frac{V_G}{2V_S}. \quad (18)$$

Thus, microenvironmental variation is implicitly included in the model. Note that if V_E is varying in space, r_e and K_e in equation (18) vary in space. This means that a spatially increasing environmental variance is mathematically equivalent to a spatially decreasing maximal intrinsic growth rate and a spatially decreasing carrying capacity, as described by equations (16)-(17). Thus, according to equation (4), range margins may form where the environmental variance increases.

In the corresponding simulations, mating is assumed to occur randomly with discrete, non-overlapping generations. The individuals are assumed to be monoecious and diploid. The expected number of gametes that each individual contributes to the next generation (i.e., the expected number of offspring) is determined by its fitness, which is defined as

$$W(z, N) = 2e^{r(z, N)}. \quad (19)$$

Here, $r(z, N)$ is given by equation (14). The factor 2 is included to account for the fact that two individuals are needed to produce one offspring. The realised number of offspring each individual produces in its lifetime is, in turn, given by a Poisson distributed random variable with expected value equal to $W(z, N)$. Thus, it is possible that an individual with a high fitness

fails to produce any offspring, or that an individual with low fitness successfully produces many offspring. The average population fitness is obtained from the expected value with respect to the phenotype distribution of equation (19)

$$\bar{W}(\bar{z}, N) = 2 \sqrt{\frac{V_S}{V_S + V_P}} \exp\left(r_m \left(1 - \frac{N}{K}\right) - \frac{(\bar{z} - \theta)^2}{2(V_S + V_P)}\right). \quad (20)$$

An alternative way to write equation (21) is

$$\bar{W}(\bar{z}, N) = 2 \exp\left(r_m \left(1 - \frac{N}{K}\right) - \frac{(\bar{z} - \theta)^2}{2(V_S + V_P)} - \frac{1}{2} \ln\left(1 + \frac{V_P}{V_S}\right)\right). \quad (21)$$

When $V_P \ll V_S$, it follows that (cf. equation (14))

$$\bar{W}(\bar{z}, N) \approx 2 \exp\left(r_m \left(1 - \frac{N}{K}\right) - \frac{(\bar{z} - \theta)^2}{2V_S} - \frac{V_P}{2V_S}\right). \quad (22)$$

Thus, the continuous and discrete models agree when the phenotypic variance is low relative to the intensity of selection. For high phenotypic variance, there could be deviations between the equilibrium genetic variance obtained in simulations and the prediction for the continuous model at linkage equilibrium, which is $V_G = b\sigma\sqrt{V_S}$ (Barton 2001; Fouqueau & Roze 2021). Here, b is the steepness of the environmental gradient, that is, the derivative with respect to space of θ .

Note that in Barton (2001), Polechová & Barton (2015), and Polechová (2018), as well in the papers in this thesis, it is assumed that a single quantitative trait is under selection with respect to an environmental variable that varies in space (except for **Paper IV**, where multiple traits are under selection). Unless otherwise stated in the papers, it is furthermore assumed that the locally optimal trait value is given by a function that has a horizontal inflection point in the centre of the habitat and is steepening towards the edges of the simulated habitat. In my simulations, this steepening function is a cubic polynomial $\theta(x_i) = Ax_i^3 + Bx_i^2 + Cx_i + D$ (Figure 4). The specific values of the coefficients are different in the different papers depending on what is most suitable for the aspects that are studied. Note that I usually neglect temporal variation in the optimal trait value, with the exception of random temporal fluctuations in **Paper II**. For simplicity, the gradient in optimal phenotype is referred to as the environmental gradient in the papers. However, I stress that the optimal phenotype probably does not depend linearly on the physical environmental gradient in natural ecosystems (see discussion in the ‘Relevance of models to natural populations’ subsection below).

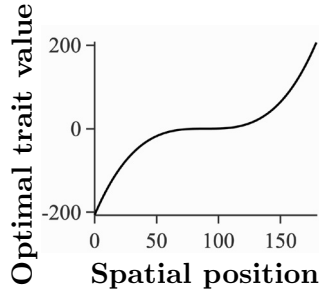


Figure 4: Illustration of how the gradient in the optimal trait value steepens towards the edges. The gradient shown in this figure is the gradient in optimal trait value used in **Paper I**.

Mutations and genetic architecture

As stated above, the individuals are assumed to be diploid. The genotype of each individual is assumed to consist of multiple bi-allelic loci with additive allele effects. Mutations between the two possible alleles occur symmetrically and reversibly with equal probability μ . Recombination between loci occurs freely (i.e., with probability $\frac{1}{2}$ between any pair of loci), except in **Paper I**, where tighter linkage between neighbouring loci is further studied (i.e., recombination rate between neighbouring loci is fixed to a value between 10^{-5} and 0.5). Note that although the allelic effects are additive for the trait value, they are not additive for fitness because fitness is a non-linear function of the trait value. In particular, there may be implicit dominance and epistatic effects depending on the relative positions of the realised trait value and the local optimum.

Relevance of the models to natural populations

A critical reader may object to the choice of a smoothly steepening function to describe how the optimum in the trait value varies in space. To motivate the choice of a smooth function, recall that the model implicitly contains fine-grained spatial variability (because V_E is implicitly included in r_m and K). Thus, the function $\theta(x_i)$ can be considered to describe the average optimal trait value in the discrete deme i . If there are larger spatial discontinuities in the habitat, local range margins could form. In this case, as explained in Bridle et al. (2019), the simulated habitat may be considered to represent the habitat of a local population rather than the habitat of an entire species. Local populations, for example of the snail *L. saxatilis* (Butlin et al. 2014), may undergo evolution on the microhabitat level, and the equation determining the critical steepness of the environmental gradient, equation (4) (see Introduction) describes where evolution does not allow further range expansion of these local populations. Using equation (4), one can predict the maximal equilibrium geographic extent of evolving local populations and therefore also obtain an indication of how important a local population may be as a demographic source (and hence which localities are likely to be most important for conservation efforts). The entire range of the species is the collection of all local populations including metapopulation dynamics (Holt & Keitt 2000; Harding & Namara 2002; Roy et al. 2008). Furthermore, it is necessary to first understand simple situations, such as range expansion along a smooth gradient, in order to understand more complex situations. Finally,

temporal fluctuations, which would distort the smoothness of the gradient, were studied in **Paper II**.

There are several reasons for using a steepening function to describe the optimal trait value, rather than (for example) a function that changes linearly in space. First, and most importantly, it is known from previous work (Polechová & Barton 2015; Bridle et al. 2019) that range margins may occur where the effective environmental gradient is steepening, whereas no range margins occur when all parameters in equation (4) are constant. Thus, a steepening gradient makes it possible to automatically find the point where adaptation fails. While I choose to vary only the steepness of the gradient in optimal phenotype (b) in my model, other parameters, such as K and σ , could vary in space as well, which could also lead to the formation of range margins. For instance, the presence of a competing species could be realised as a decreasing K because the population would have to share limited resources with another population. The choice to let b vary in space, while keeping K and σ fixed was done for simplicity to reduce the number of parameters that needs to be varied. One would expect the same results (i.e., range margins forming where equation (4) is satisfied) if, for example, b is kept fixed while K is varying in space.

Second, in nature, it is not necessary that the gradient is monotonically steepening, as assumed in the model. According to equation (4), it is sufficient that the environmental gradient steepens locally for evolution to fail and range expansion to stop. A globally steepening gradient in the simulation models is used for convenience. A more realistic gradient with a varying steepness would allow range expansion until the inequality in equation (4) is satisfied. It is, however, worth to point out a caveat here. If the geographic region where equation (4) is satisfied is very narrow relative to the average dispersal distance, individuals in the population could potentially disperse across this region and establish another population on the other side of the unfavourable region. Thus, equation (4) needs to be satisfied for a sufficiently wide geographic range for range margins to form.

Third, there are many examples of physical environmental gradients that are indeed steepening. For example, there is a steepening gradient in (decreasing) salinity in the Baltic Sea as one moves southwards along the Swedish west coast and down through the Øresund (Johannesson et al. 2020). Consistent with the expectation from equation (4), the range margins of many marine species ends right where the gradient in salinity is steepest (Ojaveer 2010). This is, for example, true for all species of wrasse found in Scandinavia (Halvorsen et al. 2021).

Fourth, the physical forces that act on an individual may scale non-linearly with the environmental conditions, creating a steepening gradient in optimal trait value even when the physical properties change linearly in space. For example, drag force from flowing water, acting on animals living in streams or on wave-swept shores, scales quadratically with the flow velocity (Denny 1999). In addition, the physiological effects of the environment may be non-linear. For example, trait values may be phenotypically buffered (kept constant) in environments that individuals are commonly exposed to (Otaki et al. 2010; Reusch 2014; Walter et al. 2022). However, outside the normal range of conditions, homeostasis may be disrupted resulting in stressful physiological effects (Chevin et al. 2010), which might be experienced as a steepening gradient in optimal trait value.

Finally, more than one trait may be involved in local adaptation. It might be sufficient that the optimal trait value corresponding to a single one of these traits is increasing in an accelerating manner for range margins to form. This is a topic investigated in more detail in **Paper IV**.

Main results and discussion

Paper I - The effect of the recombination rate between adaptive loci on the capacity of a population to expand its range

In **Paper I** (Eriksson & Rafajlović 2021), it is investigated how the range expansion capacity of a population is affected by the recombination rate between adaptive loci and by the allowance or disallowance of selfing. In agreement with Peischl et al. (2015), it is found that range expansion is slowed down when the recombination rate between the adaptive loci is reduced (Figure 1 in **Paper I**). In some cases, range expansion is also slowed down when selfing is allowed, probably due to increased expression of recessive and deleterious alleles in comparison to when selfing is not allowed (Crow & Kimura 1970).

Nevertheless, it is found that reduced recombination slightly increases the equilibrium range in comparison to when recombination between the adaptive loci is free. However, the range increases by only a few demes, typically corresponding to a 10% increase in the effective environmental gradient at the range margin, with the largest effect observed when selfing is not allowed (Tables S1, S3, and S12 in **Paper I**). This increase in the equilibrium range is likely due to blocks of alleles acting as ‘super-genes’ that are under stronger selection than single alleles (Mérot 2020), which effectively increases the right-hand side of equation (4). A similar result was observed by Polechová & Barton (2015) when the effect sizes of alleles were randomly distributed rather than bi-allelic; alleles of large effect accumulated at the range margins and allowed for slightly larger range than for bi-allelic loci (Polechová & Barton 2015).

While the increase in equilibrium range due to reduced recombination is modest (suggesting that the findings by Polechová & Barton (2015) are relatively robust to variation in recombination rate), a low recombination rate may have additional transient but long-lasting positive effects on geographic ranges. Notably, in **Paper I** it is shown that when the recombination rate is low, genetic variance within the population is preserved better than when recombination is free. This could facilitate range expansion, especially when the population has a large amount of standing genetic variation (Figure 4 in **Paper I**). Indeed, as seen in Figure 1 in **Paper I** range expansion may, when the genetic variance is inflated, proceed beyond the point where local adaptation is expected to fail. Moreover, when the recombination rate is low, the population persistence-time beyond the expected equilibrium range could be increased by up to 100,000 generations (Figure 3 in **Paper I**). Unless the generation-time of the organism is very short, this time is likely to be longer than the time during which the environmental conditions can be assumed to be temporally constant. Thus, a low recombination rate may substantially increase the range of a population, and although this effect is transient, it may last for long enough to appear as an equilibrium range in natural populations. A potential consequence of this is that genomic regions of low recombination could help populations to cross short barriers where equation (4) is satisfied (Figure 5). The simulations in **Paper I**, thus, support the empirical observations that low recombination rates may facilitate local adaptation (Wellenreuther & Bernatchez 2018; Faria et al. 2019).

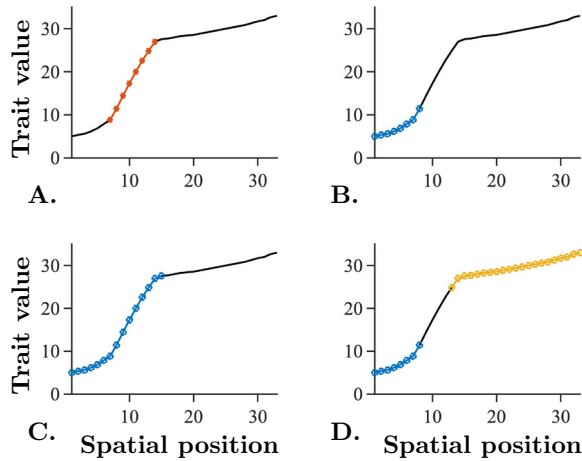


Figure 5: A possible mechanism for how genomic regions with low recombination rates may facilitate larger geographic ranges in equilibrium. A short stretch of an environmental gradient where equation (4) is satisfied (red stars in panel A) may act as a barrier for range expansion. The range of the population (blue rings) initially ends where the gradient becomes too steep (panel B). However, when the genetic variance is temporarily increased, for example due to hybridisation (cf. Kirkpatrick & Barrett 2015), the population may transiently occupy the steep region of the gradient (panel C). If the population persists in this region for long enough, which may be made possible when the recombination rate between adaptive loci is low, this may allow colonisation of the shallower part of the gradient to the right. When the range eventually contracts, it will contract only from the steep part of the gradient, leaving the two populations living along the shallower parts of the environmental gradient intact (blue and yellow rings in panel D). Note that the average trait values of the two local (blue and yellow) populations may be very different.

Consistent with empirical data (Griffin & Willi 2014; Hargreaves & Eckert 2014), it is also found in **Paper I** that when selfing is possible, the range can be increased considerably in comparison to the range for populations with obligate outcrossing. In **Paper I**, it is argued that this is because one of the advantages of selfing in range margins is that selfing provides reproductive assurance, and thus ameliorates the Allee effect that is caused by difficulty of finding a mate in sparse populations. In particular, when selfing is possible, a single individual, which happens to migrate to a distant habitat patch, may establish a local population. This population may persist under environmental conditions where local adaptation is expected to fail because it experiences relatively low gene flow from surrounding populations. This is in part because the population tends to be surrounded by demographic sinks, but also because it may have a relatively high local population density, especially if the founding individual by chance happened to be well-adapted to the local environment (**Paper I**; cf. also Rafajlović et al., 2017).

Paper II - The role of phenotypic plasticity in the establishment of range margins

In **Paper II** (Eriksson & Rafajlović 2022), it is investigated how phenotypic plasticity affects range margins when there is a cost for being plastic. In this paper, evolution of plasticity is modelled similarly to how it is done in the models by Leimar et al. (2019) and Schmid et al. (2019), but with range expansion occurring over a steepening environmental gradient. The

main finding of **Paper II** is that there are three qualitatively different outcomes for the equilibrium range that are possible depending on the shape and magnitude of the cost-related function for plasticity and the strength of selection relative to drift at carrying capacity (Figure 6).

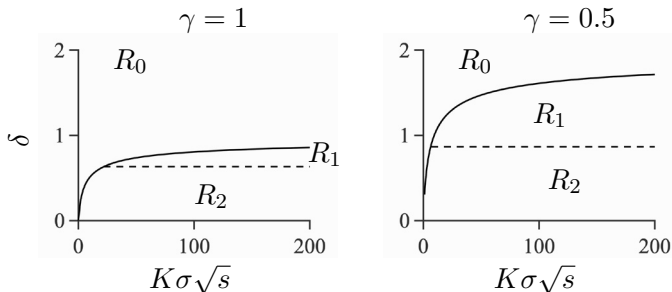


Figure 6: The main result in **Paper II** is that the equilibrium range of a population that can evolve costly plasticity falls in one of three regimes with respect to the cost of plasticity and the compound parameter $K\sigma\sqrt{s}$, which is the strength of selection relative to drift at carrying capacity. In regime R_0 , the potential to evolve plasticity does not increase the range of conditions where the population may remain adapted, i.e., the evolution of plasticity does not change equation (4). In regimes R_1 and R_2 , the potential to evolve plasticity may increase the geographic range where local adaptation is possible. While the range is still limited in regime R_1 , it may expand without bounds for parameters within regime R_2 because perfect plasticity may evolve. The relative sizes of the regimes depend on the shape of the cost-related function (which is defined as $C_\gamma(g, \delta) = (1 - \delta|g|)^\gamma$ in **Paper II**, where g is a measure of the plasticity of the individual, and where δ and γ are the scale and shape parameters for the cost-related function; the cost is realised by multiplying $C_\gamma(g, \delta)$ to the individual's fitness). That is if the cost-related function is concave ($\gamma < 1$) or convex ($\gamma > 1$). The size of regime R_1 is larger the more concave the cost-related function is.

For parameters in regime R_0 , zero plasticity is optimal under all environmental conditions until local adaptation fails. This causes range margins to form before any significant plasticity evolves. In regime R_1 or R_2 , plasticity may evolve under conditions when equation (4) is not satisfied and this may increase the extent of the range substantially because plasticity effectively reduces the steepness of the environmental gradient. For regime R_2 , there is no evolutionary limit to the equilibrium range of the population. Note that parameters in regime R_0 does *not* imply that evolution of positive plasticity never occurs. For example, in regime R_0 , some plasticity may evolve at the expansion front or in range margins due to maladaptation, as explained in Chevin & Lande (2011). However, in regime R_0 positive plasticity is restricted to locations where the population is maladapted, whereas in regimes R_1 and R_2 populations can be both locally well-adapted and plastic. The concavity of the cost-related function determines how large the R_1 -regime is relative to the other regimes (i.e., larger R_1 -regime for more concave cost-related functions). Because plasticity is commonly occurring in natural populations, even under non-extreme conditions, it is likely that most parameters are within the R_1 regime.

In habitats with temporally fluctuating environmental conditions (where the environmental cues sensed during the development of the plastic response, for simplicity, are assumed to perfectly agree with the optimal phenotype during selection), it is found in **Paper II** that relatively strong plasticity may evolve even when the environmental gradient is close to zero

(that is, in the vicinity of the source of the expansion). This plasticity can considerably increase the speed of range expansion (cf. Figure 2C and Figure 3C in **Paper II**), despite the fact that temporal fluctuations in the environmental conditions lead to an overall smaller population size in the model. Notably, the plasticity that evolves differs between local populations throughout the range, for both static and the temporally fluctuating environmental conditions. Higher plasticity evolves in locations with steeper gradients and close to range margins, suggesting that it is common that plasticity varies geographically in natural populations (in accordance with empirical data; e.g., Münzbergová et al. 2017; Rugiu et al. 2018).

It is worth pointing out that the empirical evidence for costly plasticity has been elusive, suggesting that plasticity may not in general be costly (Murren et al. 2015). However, in **Paper II** it is argued that if the cost-related function is strongly concave, costs may be very small unless plasticity is too extreme, which may partly explain the difficulty to empirically detect costs of plasticity. It is also known that the predictability of temporal fluctuations limits the evolution of plasticity (Bitter 2022). Unreliable environmental cues may be realised as a form of cost of plasticity. I thus expect that unreliability of the environmental cues would have an effect on the range expansion dynamics that is similar to that for costly plasticity. A more detailed exploration of how cue reliability affects the establishment of range margins by limiting the evolution of plasticity is an important topic for future research.

Paper III - Adaptive, maladaptive, neutral, or absent plasticity: Hidden caveats of reaction norms

Recall that plasticity may be adaptive or non-adaptive. In **Paper III** (Eriksson et al. 2022), it is investigated when it is possible to conclude that plasticity is adaptive from empirically measured trait values. In reciprocal transplant experiments, individuals from each of two different populations are transplanted from their native environment into the environment that is the native environment of the other population (or transplanted back into their own native environment, as a control), and *vice versa* (Johnson et al. 2022). The trait values of interest are subsequently measured, and reaction norms (Chevin et al. 2010) for the phenotypic expression of the traits are obtained. However, the correct interpretation of reaction norms differs depending on whether the assessed trait is an adaptive trait (i.e., a trait under selection with respect to the environmental variable in question), or is an indicator of fitness (i.e., a trait that is correlated to the individual's fitness and is kept constant in non-stressful environments). When plasticity is adaptive, the trait values of adaptive traits should change, whereas the trait values of fitness-indicator traits should remain constant. Yet, in some studies, *any* change in the trait value of the measured trait has been interpreted as evidence for adaptive plasticity. As pointed out by Bonser (2021), this may lead to erroneous conclusions when a fitness-indicator trait is incorrectly assumed to be adaptive. When the assessed trait is a fitness-indicator, the observed plasticity in the trait is just a passive consequence of being in a stressful environment (recall the discussion in the introduction). Therefore, plasticity in the measured trait indicates low environmental tolerance and not adaptive plasticity. The issue has verbally been pointed out by Reusch (2014) and by Bonser (2021), but to the best of my knowledge, it has not previously been formally theoretically investigated.

A problem with empirical studies is that it may not be known *a priori* whether the measured trait is better described as an adaptive trait or as a fitness-indicator trait (intermediate possibilities on a continuous spectrum may exist, but one of the two possibilities may be closer to reality than the other). In simulated populations, unlike in natural populations, it is known how much plasticity the population possesses and whether the plasticity is adaptive or not. Therefore, simulations can be used to illustrate when the possible outcomes from reciprocal transplant experiments occur. The main aim of **Paper III** is to determine when it can be expected that reciprocal transplant experiments, and the resulting reaction norms, can give clear evidence for or against *adaptive* plasticity. To this end, the simulation results from **Paper II** are used to mimic reciprocal transplant experiments *in silico*.

Empirical data from the marine isopod *Idotea balthica* (Figure 7; De Wit et al. 2020) are further used as a showcase to demonstrate the points from the theoretical model. The empirical data show that *I. balthica* from the south of the Öresund, in a low-salinity environment of 8 practical salinity units (psu), has reduced grazing rate and increased metabolic rate when transplanted to the north of the Öresund, in a relatively higher salinity of 16 psu, whereas individuals from the high-salinity environment do not have any significant difference in grazing rate or metabolic rate when transplanted to the low-salinity environment. It is not obvious whether grazing or metabolic rate by themselves are to be considered as adaptive or as fitness-indicators. From the model results, it can be seen that both possibilities are plausible. However, for physiological reasons, it is argued in **Paper III** that it is unlikely that reduced grazing is adaptive when it occurs at the same time as the metabolic rate is increased.



Figure 7: The isopod *Idotea balthica* exhibits a wide range of phenotypes. This species does not disperse during the larval stage (De Wit et al. 2020) and has a remarkably high tolerance to various salinity levels (Leidenberger et al. 2012; Panova et al. 2017), making it an ideal model species for studying local adaptation and plasticity (Wood et al. 2014; Rugiu et al. 2018, 2021). Photo credit: Pierre De Wit.

The paper concludes by listing four caveats and recommendations:

- The interpretation of reaction norms differs depending on what kind of trait is measured (i.e., whether it is an adaptive trait or a fitness-indicator trait).

- Phenotypic buffering need not be perfect (i.e., reaction norms in phenotypically buffered fitness-indicator traits need not be flat). When such ‘sub-optimal’ phenotypic buffering occurs, it might be possible to distinguish between fitness-indicator traits and adaptive traits from the direction of the reaction norms (e.g., reaction norms suggest that the measured trait is a fitness-indicator when the trait values change in the same direction for both populations when they are transplanted from their native to their non-native environment).
- Experiments conducted under laboratory conditions may not capture the full complexity under natural conditions. For example, an adaptive response under laboratory conditions may not be adaptive with respect to some additional selection component that occurs under natural conditions but is not considered in the experiment.
- Carefully tailored simulations may aid the interpretation of empirical data.

Paper IV - Species’ ranges and the steepening-gradient hypothesis

In **Paper IV** (Tomasini et al. 2022), it is investigated how the joint effects of different components of environmental selection acting on separate adaptive traits affect the range expansion capacity of a population. A particular focus in **Paper IV** is on situations with two adaptive traits, one with a steepening gradient in the optimal trait value and the other with an optimal trait value that changes linearly in space (i.e., a gradient in optimal trait value with a constant gradient). This is because when a single adaptive trait is under selection, a steepening gradient in the optimal trait value will inevitably result in the failure to adapt locally, whereas adaptation can be unlimited when the trait optimum changes linearly in space (Polechová & Barton 2015). It is found that the two environmental gradients reinforce each other, causing the overall environmental gradient to be steeper than each of the individual gradients. Moreover, range margins necessarily form, because one of the two gradients is steepening in space. This is true over the whole range attainable by the population, even when the steepening gradient is shallower than the gradient for the trait with a constant gradient. The results from **Paper IV** thus strengthen the plausibility of the steepening-gradient hypothesis as an explanation for why range margins of species form. Because multiple environmental factors are likely to contribute to the overall selection, the combined effects of all gradients may result in a very steep overall gradient. Interestingly, even when just one of these individual gradients is overall shallow but slightly steepening, this can be sufficient for the establishment of stable range margins. This result demonstrates the importance of shallow environmental gradients which can be overlooked in environmental association studies (Rellstab et al. 2021)

Moreover, it is investigated in **Paper IV** how range expansion dynamics are affected when the overall environmental selection acts on a single adaptive trait, compared to when the same environmental selection is decomposed into separate components, where each component acts on a separate trait. The traits were assumed to be orthogonal (*sensu* Fisher’s geometric model; Fisher 1930). For the parameter values studied in **Paper IV**, it is found that when the selection pressure is decomposed between multiple orthogonal traits, the fitness-cost for deviating from the optimal phenotype is lower than when the same selection acts on a single composite trait. Consequently, the range attained is larger in the former than in the latter case. Although the difference measured in the number of demes is not large, the difference is apparent in terms of

the critical gradient (up to 18%; refer to Table 2). This suggests that a population under stressful conditions may benefit from decomposing the environmental selection into multiple components acting on separate orthogonal adaptive traits. In other words, a larger number of orthogonal adaptive traits may potentially allow a population to attain a larger geographic range compared to when the number of adaptive traits is smaller. Indeed, there is empirical evidence for range expansions being associated with evolution of novel traits (Santos 2017), but outlining the theoretical details is the subject of future studies. Future research is also needed to explore how pleiotropy and various patterns of recombination rate between loci underlying separate adaptive traits may affect the range expansion capacity when the traits are subject to different components of environmental selection.

Reflections and outlook

Understanding the evolutionary mechanisms behind range expansions and range margins is important both for shedding light on fundamental scientific questions, such as understanding speciation (Weir & Price 2011; Gilbert et al. 2022), as well as for tackling challenges related to global change (Di Marco et al. 2018; Pinsky 2020; O'Hara et al. 2021; Sala 2021; Wilson & Fox 2021). A particularly important and urgent application for the modelling of evolution at range margins is the prevention of biodiversity loss in the face of global climate change. By identifying the factors that limit evolution at range margins (addressed in **Paper I**, **Paper II**, and **Paper IV**) and by accurate measurement of these factors (addressed in **Paper III**), management and conservation practices could potentially be designed to better mitigate the negative consequences of climate change on biological communities. For instance, climate change is expected to cause large-scale movement of many species, including potentially invasive species (Beaury et al. 2020; Rathee et al. 2021). As discussed in **Paper II**, invasive species often exhibit a high degree of plasticity (Geng et al. 2007; Ren et al. 2020). Thus, identifying the ecological factors that promote the evolution of plasticity could be a part of containing the spread of some invasive species. For example, reducing the dispersal capacity for invasive species would not only directly prevent their spread but also potentially suppress the evolution of plasticity (Figure 6).

Despite the advances made in recent years, including the work done within the framework of this doctoral thesis, there are still gaps in the theoretical understanding of the evolution of species' ranges. In the following, I discuss three important questions that are yet to be resolved (and I stress that I certainly do not claim that I think these questions are the only ones that are interesting to consider).

All my papers, as well as many other similar studies such as Polechová & Barton (2015) and Benning (2022), one-dimensional habitats are assumed. Yet, although some important habitats are approximately one-dimensional, most natural habitats are two-dimensional. Because no terms related to allelic effect sizes or selection occur in the analogous equation for two-dimensional habitats (equation (6); Polechová 2018), it would be interesting to investigate whether the results in my thesis hold in two dimensions or if they are particular features related to one-dimensional habitats. Low recombination may, for example, allow for wider equilibrium ranges in one-dimensional habitats because 'super-genes' may be under stronger selection than freely recombining loci, but this effect may not carry over to two-dimensional habitats because the effect sizes of alleles do not affect the equilibrium range in two dimensions (cf. equation (6) and equation (4)). According to the results of **Paper I**, the major advantage of low recombination, however, does not seem to be that it alters equation (4), but rather that it increases the persistence time under conditions when local adaptation is predicted to fail. Therefore, low recombination might still have a substantial positive effect on geographic distributions even if it does not have any effect on the equilibrium range in two-dimensional habitats. However, the precise role of the spatial dimensionality of the habitat, especially on the results from **Paper I** and **Paper IV**, remains an intriguing open question for future work.

In my thesis, I have focused on spatially varying but temporally constant habitats, except for the stochastic temporal fluctuations considered in **Paper II**. How range margins are altered when there is a systematic trend in the environmental conditions is therefore an important topic for future research, especially in combination with the theory for range expansion along multiple environmental gradients considered in **Paper IV**. Species that shifts their range due to climate change may be faced with new conditions in other variables than temperature. For example, daylight conditions remain unchanged even when the climate changes, and therefore a species that follows its optimal temperature may need to adapt to novel levels of daylight (Ittonen et al. 2022).

Finally, an important factor that often contributes to the establishment of range margins is interaction with other species (e.g., O'Brien et al. 2017; Simonsen et al. 2017; Freeman et al. 2022). Intra- or interspecies interactions, such as competition, predation, or symbiosis, may alter the effective environmental gradient, the carrying capacity that a species is experiencing, and/or create trade-offs between different traits (Case et al. 2005; Alexander et al. 2022; O'Brien et al. 2022). Exactly how these interactions shape the environmental gradients for each species when multiple species are evolving jointly remains an open question. For example, a trait may be favoured by the abiotic environment but may increase the risk of predation (e.g., by rendering the individual more visible) or be a disadvantage in competition. Thus, it may not be obvious from a single abiotic environmental property, such as temperature, where the distribution of a species ends.

It will be very exciting to follow the further advances within the field in the coming years, including progress in the research directions I have outlined above.

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